LIMITS OF RESPONSE TO SELECTION

by

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Submitted to the University of Edinburgh as a Thesis, in fulfilment of the requirements for the degree of Doctor of Philosophy.

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OCTOBER, 1961.

LIST OF CONTENTS

		Page
I.	AIMS	1
II.	INTRODUCTION	1
III.	MATERIAL AND METHODS	15
	The Stock	15
	The Character	15
	The Experiments	16
	a. The full-sib lines	16
	b. The mass-mated lines.	17
IV.	RESULTS	22
	The full-sib lines	22
	The mass-mated lines	24
V.	SCALE	33
	Genetic variation	33
	Non-genetic variation	36
VI.	DISCUSSION	46
VII.	SUMMARY	58
	TABLES	
	FIGURES	
	REFERENCES	
	ACKNOWLEDGEMENTS	

I. AIMS.

(a) To test the effect of chance fixation on the ultimate limit.

(b) To test the effect of restriction of the population size on the limit.

II. INTRODUCTION.

Despite the large number of publications dealing with selection experiments on quantitative characters, the effects of chance fixation and restrictions on population size, although theoretically considered, have not yet been experimentally explored.

It is unsafe to generalise on the genetic control of quantitative phenomena. The difficulties stem mainly from the fact that in each experimental situation there are a number of unknown quantities which reduce the reliability of predictions concerning the ultimate results or selection limits. The number of genes involved and their effects, their frequency and linkage relationships, the past evolutionary history of the particular populations, the existence of multiple alleles, are all complicating elements.

Cases are found in which selection was ineffective, others where continued progress was maintained for many generations and in which the plateau phase was attained with a partial or complete exhaustion of genetic variability.

The characters to which selection has been applied, in domestic as well as laboratory animals cover a very wide range.

In pointing out some of them we have chosen either the most representative or the ones which have made the greatest contribution to the understanding of quantitative inheritance.

In domestic animals it is perhaps interesting to refer to the data presented by Lush (1951) referring to fleece weight in Australian Merinos, butterfat in New Zealand Jerseys and butterfat percentage in Dutch Friesians. Although the data do not refer to properly designed experiments, and it is not possible to partition the improvement into environmental and genetic components, it should be noted that even during the two world war periods, there was no detectable reduction in the butterfat percentage of Dutch Friesians. This can perhaps be accounted for by the fact that fat percentage is a highly heritable character (a heritability of around 50% and consequently more responsive to selective pressure) or else because, being a percentage measurement, it is less affected by the nutritional level than is milk yield.

The same kind of results are shown for butterfat percentage by the Danish cow testing association. The periods of food scarcity did not affect the increasing trend in butterfat percentage of the milk.

Lush (op. cit.) gives a detailed account of the results obtained with pigs in the official testing stations in Denmark. The response to selection, although with different magnitudes in the different characters selected, is always present. Feed requirements in the beginning of the experiment and the characters

related to carcass quality - body length and thickness of back fat - have the largest responses to selection pressure.

Sierk and Winters (1951) selecting for economically important characters in swine and culling on the basis of numbers of pigs farrowed, numbers of pigs weaned, rate of gain up to 154 days of age, efficiency of feed utilization and score were not able to promote any progress. This absence of response can be understood by a consideration of the selection criteria involved, and of the mating system applied which was intended to increase the level of inbreeding as rapidly as possible.

Dickerson (1951) reports a similar situation in a selection experiment again for economic characters in swine. It is pointed out that selection is effective for some characters, e.g. body dimensions and carcass conformation but almost negligible for other characters, such as viability and litter size which have apparently been subjected to an appreciable degree of unidirectional selection. Negative physiological association between different selected characters have been shown to exist, and the increased level of inbreeding acts as a brake on performance. These conditions produce a situation referred to by Lerner (1954) as comparable to "Alice in Wonderland" or by Dickerson (1955) as "genetic slipage".

Terril (1951) selecting for economcially important traits in sheep was able to show that the genetic improvement from 1938 to 1958 in inbred Rambouilet lines although present was less than expected and that the greater part of it was obtained from the selection of rams.

Robertson (1949) in a report dealing with a herd of Fulani cattle at Shika in Nigeria selected for increased milk yield during 18 years, points to the very creditable selection pressure achieved and the probable yearly genetic improvement of the order of $2^1/2$ gallons of milk. However, in practice it is not easy to distinguish between genetic improvement and that brought about by better management methods. This aspect is very marked in selection experiments with tropical or sub-tropical cattle, where not only changing conditions of management but climatic irregularities are sources of variation. In this respect the Pusa herd of Sahiwal breed with the phenomenal increase in production is perhaps the best example of environmental masking of any possible genetic improvement achieved, Sayer (1934a, 1934b, 1937). Dempster and Lerner (1947) selecting for egg production in the fowl and testing for the relative efficiency of different breeding methods pointed out, not unexpectedly, the need for the widespread use of younger birds as parents. The optimal level is when 90% of the females and 80% of the males are pullets.

Lerner and Hazel (1947) analysing the same data showed that the rate of progress was predictable thereby proving the validity of the genetic and statistical assumptions upon which the predictions were based.

Lerner and Dempster (1951) selecting for shank length in the fowl showed that a plateau following an initial marked response was achieved but that neither the amount of genetic

variance nor the degree of heritability decreased. In fact if a correction for the degree of inbreeding in applied to the figures obtained the calculated heritability is bigger during the plateau phase. It is also shown that the number of offspring raised to maturity per dam - which is presented as an index of fitness - falls from 3.75 in the first phase to 2.47 during the plateau and that a negative correlation between the genotypes of the dams for shank length and hatchability of their eggs developed during the second phase of the experiment. Half of the loss in the rate of progress in this second phase is ascribed to that of negative correlations.

For economic reasons as well as biological suitability, selection experiments using laboratory animals are much more abundant, and the variety of aims is also larger than those of the domestic species.

Mather and Harrison (1949) selecting for increased number of sternopleural bristles on Drosophila melanogaster in a long and laborious experiment proved the importance of linkage and presented good evidence of the concepts of polygenic or quantitative variation, Mather (1941, 1942).

Robertson and Reeve (1952 et. seq) selecting in prolonged experiments, for wing and thorax length on Drosophila melanogaster were faced with complex genetic situations which did not fit any simple theory. F.W. Robertson (1955) reports that the line selected for small thorax in reaching the limit or plateau phase gave evidence of fixation. Not so in the line

selected for increased thorax in which reversed selection or relaxed selection resulted always in a return toward the original thorax size.

Clayton et al (1957) selecting for abdominal bristles were able to show the existence in 7 out of 10 lines of lethal autosomal genes in high frequencies which were perhaps responsible for the existing genetic variance. It can be assumed that these genes or factors had a favourable effect on the character when in a heterozygous state, so that an overdominance situation occurred when the effects of artificial and natural selection were considered together. This aspect of heterozygous advantage has been reported in economic characters in poultry, Briles (1954). Egg production in 3 inbred lines of White Leghorns being from 9 to 30% higher for birds heterozygous for the B blood group locus.

Goodale (1938) selecting for increased body weight on mice, was able to shift the mean of the base population by 40% in males and 32% in females.

MacArthur (1949) selecting for increased and decreased body size in mice was also able to effect a marked change in the mean size and, as pointed out by the author, it is quite surprising how rapidly an organism can be remodelled by a short term of mass selection in such fundamental characters as growth and reproduction.

Falconer and King (1953) crossed the lines for increased size created by Goodale and MacArthur, both considered to have reached a limit, and selection was restarted. The line created by the cross outdid the limit of the highest parental line after

about 8 generations.

The renewed response in the cross-bred line was interpreted as showing that exhaustion of genetic variance was the reason behind the limit achieved in the parental lines. It is also shown that this genetic exhaustion was mainly due to the effects of selection. Only a small part of the loss could be imputed to the effects of inbreeding.

The pattern of response was directly comparable with that obtained by Falconer (1953) when the selection was started from a four-way cross of inbred lines to which no previous selection had been applied.

Falconer and Latyzewski (1950) modified by Falconer (1960) selecting for size in mice on restricted and unrestricted planes of nutrition showed how important a switching mechanism for polygenic systems, the environment can be. The mice selected under unrestricted feeding when raised on the poor plane of nutrition did not reach the weight of contemporaneous mice of the restricted diet line. On the other hand mice of the restricted diet line when raised on full diet showed that the improvement achieved was almost identical to that obtained by mice selected on full-diet. An analysis of the fatness of the mice of the two different lines when both were reared under full-diet showed that the mice of the line selected under restricted feeding were less fat than the ones selected under full-diet. And more, "the difference in the weight of fat was greater than the difference in total body-weight, so that

weight of non-fat tissues was actually greater in the restricted line".

Clarke, Maynard-Smith and Sondhi (1950) selecting for rate of development in Drosophila subobscura came to the situation which is suggested to be a "developmental barrier". No progress or very little was achieved in selecting for a faster development. And as said by the authors this is perhaps a situation which may prove to be typical of characters which have in the past been exposed to directional selection for an appreciable time in a reasonably large population, either in nature or in domestication.

And this "developmental barrier" is perhaps a more definite than the one reported by F.W. Robertson (1955) who, in explaining the limit achieved in the small lines, (referred to earlier), suggested that the small size of these lines resulted from a low metabolic efficiency provoked by homozygosis. There are perhaps other genes or gene combinations in the base populations which could, if present in the selected lines, promote smaller thorax than the ones achieved.

It is not surprising that the results achieved in these experiments are not directly comparable. Even if the genetical mechanisms concerned could be thought to be the same, the underlying physiology of the different characters must be widely different and the diversity of the breeding procedures is only another complicating mechanism. Still another one is the selected character itself.

It is to be expected that if a character has been submitted

to the action of natural selection no artificial selection pressure is likely to succeed since no additive genetic variance will be available. In other words if the character is closely related with natural fitness no marked response is to be achieved from selection with either farm or laboratory animals, Robertson (1955).

A further complication is the possible existence of multiple alleles. And even if this possibility has not been overlooked by quantitative geneticists (Goodale, 1938) its consequences were underestimated or neglected and mainly so by research workers with Drosophila. Drosophila, where crossing-over is non-existant in the male and which has a smaller number of chromosomes than the other laboratory animals, is perhaps more prone to show discrepancies between replicated lines or samples taken from the same population.

However, it is perhaps legitimate to think that the need for replication, in order to achieve a better sampling of the population under study, could be of more general use.

Work with blood group loci in recent years has shown the existence of some extremely large allelic series. Examples of this are the B and C systems in cattle, Stormont, (1959) and the B system in the fowl, Briles et al. (1950) where each strain or line seems to have a different series of alleles with almost no overlapping, Briles et al. (1957). It is perhaps reasonable to assume that such allelic series occur at loci occupied by genes affecting quantitative characters.

It remains to be shown whether this is true (of quantitative characters) and it is perhaps only the lack of knowledge of how to label the effect of each allele at each locus which is responsible for the omission.

And even apart from the genetic peculiarities of Drosophila and the possibility of multiple allelism the importance of replication in such selection experiments is emphasised by the magnitude of sampling variance and the possibility of gaining a better knowledge of the nature and frequencies of the genes controlling the character existing in the base population.

The replicated experiment done by Clayton et al. (1957) designed to check quantitative theories gives, apart from the main line of the experiment, good evidence of the real need of replication as a means of properly sampling the base population and so obtaining, on average, a truer picture of what happens. The selected lines in this experiment showed differences in the rate of response and in the level of plateau finally reached. These differences are perhaps due to the fact that each selection line is an independent sample of the genetic material existing in the base population or are an indication of the fact that each line is subjected, during selection, to a differential inbreeding loss of genes. For a theoretical treatment of this phenomenon see Robertson (1961). This aspect of inbreeding effects if given as an explanation by Cockerham and Martin (1958) to a similar situation found in a simulated study of selection in a computer, where the lines showing the fastest initial response

reach the plateau at the lowest level.

McBride (1959) in a replicated experiment designed to compare the relative efficiency of different selective treatments, assortative selection, mass-selection and random-mating was also able to show the usefulness and need of replications.

Rasmusson (1952) derived 10 inbred lines from a single population of Drosophila. The lines were maintained by brother-sister mating and no intentional selection was applied. In each generation sternopleural bristles and abdominal counts were made. As the result of inbreeding the lines quickly separated during the first 10 generations and the divergence achieved between the more extreme lines in both characters is of the order of 30% of the mean value of the characters in the base populations. This is the kind of picture to be expected from theoretical considerations of inbreeding effects and chance fixation. And theoretically it can be expected in a selection programme that genetic sampling or genetic drift, causing a random change in gene frequency from generation to generation, is accompanied by a directed change in the same gene frequency due to the effects of selection. In a recent paper Robertson (1960) presents a theoretical analysis of this problem. It is shown that in selecting from a large unselected base population it is the initial generation which is important in the sense of losing low frequency genes. Afterwards any of the lines created has its own genes at higher frequencies. This loss of genes and immediate increase in the remaining ones is a much

more marked process whenever there is a marked restriction in the population size - a so-called bottleneck - and in the particular case of restriction to a single pair-mating, the lowest gene frequency to be found in the offspring is 25%. It follows that no further restriction will be so powerful in provoking gene frequency changes or genetic changes by loss.

Robertson (unpublished data) selected for increased sternopleural numbers in five different lines propagated by full-sib mating, selecting as parents the best pair out of five scored. The behaviour of the lines can be best appreciated in Fig. 1. Tantaway (1959) reports a Drosophila experiment in which selection was applied for increased as well as decreased wing length. It showed parallel behaviour in the two lines selected for increase, and a lack of response to selection around the fourth generation of full-sib mating. In the down lines however, the divergence in the end of the experiment, at generation 8, between these two lines, also maintained by full-sib mating was of the order of twice the divergence from the control, of the lines selected for increased length.

The suggested explanation for this divergence in the down lines is of an environmental nature, but theoretical considerations of chance fixation and inbreeding would provide as good an argument.

Confirmation of quantitative genetical theory is not abundant. Lerner and Hazel (1947) later modified by Lerner (1954) claimed that their predictions were in good agreement

with the results obtained in their selection experiments. But, the evidence available is not entirely satisfactory, because, although the calculations of the necessary parameters used to test the validity of theory were not based on the experiment itself, the individuals upon which the calculations were made, uncles and nieces, were produced during the selection experiment.

Clayton et al. (1957) avoided the same situation by obtaining the necessary parameters from an analysis of the population in a static phase. The predictions of the response when the lines were produced and submitted to selection were reasonably good, say up to the fifth to seventh generations. The dynamic phase corresponding to selection, which through migration, within each line, from generation to generation, induced gene frequency changes and a corresponding change in the parameters so that the agreement between prediction and result, became progressively weaker.

McBride (1959), testing the effectiveness of assortative mating as an aid to selection was able to show the effect on the ultimate selection limit when the base population has a coefficient of inbreeding different of zero. Theoretically it was expected that one of the lines with an initial F value of 9.375% would show only 93% of the response of another line submitted to the same treatment. In fact the observed response in generation 5 was of the order of 82%, but at the fourth generation the response in both lines was the same and at the

end of the experiment at generation 19 the divergence of the two lines was much more marked than the theoretical prediction. The line expected to show 93% of response of the other one showed only approximately 50%. This divergence was explained by the appearance and fixation in the line that reached a higher level of a recessive gene, Scrabrosus.

Since, as previously pointed out, there is virtually no experimental evidence of the role of chance fixation and the effects of restriction of population size it was decided that a direct test on these two aspects would be useful. It was with this purpose in mind that the experiment to be described was designed.

III. MATERIAL AND METHODS

(a) The Stock.

The breeding history of the Kaduna population of Drosophila melanogaster used in these experiments has been described in detail by Clayton et al. (1957). Briefly, the population has been maintained at 25°C at a size of approximately 5000 since 1949. Before sampling the population at the start of these experiments in May 1959, roughly 175 generations of random breeding had occurred.

The sampling of the population was effected by egg collection. This was done by placing bottles containing fresh food in the cage for a period of 24 hours during which time several hundred eggs were deposited. On hatching, the young flies were sexed and transferred to 2 x 1 inch food vials.

Throughout the experiment the flies were kept in a constant temperature room (25°C ± 0.3°C).

Overcrowding in the vials or bottles was avoided by removal of the parents, and an attempt was made to maintain an optimal density of 400 hundred eggs per bottle or 50 per vial. In the initial stages the removal of parents was obligatory but at the later stages, when fertility decreased markedly, this precaution was unnecessary.

The flies were etherized for scoring and then stored in labelled tubes. When, in each case, the required sample had been scored the selection of the desired parents was straight-

forward.

The choice of breeding system and selection intensity were influenced by the results obtained by Clayton et al.(1957) and the theoretical considerations dealt with by Dempster (1955).

The Character.

In choosing the sternopleural chaetae we departed a little from the more traditional and well studied abdominals, the main reason being the relatively easier scoring technique. On the other hand it has been shown by Cooks, (1954) that the operative polygenic systems controlling the expression of sternopleural and abdominal chaeta are similar at least in part.

All the thoracic bristles and hairs are known to be directly connected to peripheral nerve cells. This was found to be true not only of wild type flies but also of mutants with either decreased or increased numbers of bristles. Stern (1938)

However, this anatomical knowledge is of not very great help to the understanding of the more or less complicated physiologico-genetical associations and the interpretation of the results of any selection experiment will, for that reason, be far from complete. On the other hand the available evidence is that both groups of bristles are under the control of polygenic systems - in other words they are quantitative characters.

The Experiments.

(a) The full-sib lines.

From the sample of the Kaduna population 32 groups of five pairs each were scored. Within each group of

five pairs the pair with the highest score was used as parents of each line.

From the progeny of each pair or line three groups of five pairs were scored, and within each group the highest scoring pair was mated. This precaution of making three sub-lines within each line was found to be of value because from the 2nd generation onwards a marked decrease in fertility occurred in almost all the lines.

This breeding system and selection procedure was followed throughout the experiment in 11 of the lines originally created.

From 11 other lines three sub-lines were similarly created in the first generation and from the progeny of each of two of these sub-lines three groups of 5 pairs were scored and the pair with the highest score was mated. Twenty-two lines were thus created, paired two by two and related in origin, by being derived from the progeny of a single pair. Thereafter, the breeding system and the selection procedure, including the creation of three sub-lines per line, were exactly the same as in the first group of 11 lines described above.

(b) The mass-mated lines.

In describing these lines we have to consider eight different groups:-

1. The C/lines.

From the Kaduna population sample we scored the sternopleural bristles of 25 pairs. The ten pairs with the

highest score were mated.

Three different lines were started C/1, C/2 and C/3. The mating procedure and the selection differential applied were the same in the three lines and were maintained until it was considered that response had ceased.

2. The B/lines.

A single pair of flies was drawn at random from the Kaduna sample and mated in a vial. The progeny were transferred to a bottle. After three days of mass-mating and laying the flies were removed from the bottle and the bottle was kept in the constant temperature room. On hatching the flies were transferred to a fresh bottle and again removed after three days of mass-mating and laying. This procedure was repeated for three more generations. In this way the progeny of the initial single mating were allowed to increase in a random mating way for five generations.

On the hatching of the fifth generation, 25 pairs of flies, the females being virgins, were scored and the ten pairs with the highest score put together in a bottle. As in the C/lines the procedure was followed until no further response to selection was obtained.

Five different lines were started: B/1, B/2, B/3, B/4 and B/5.

3. The A/lines.

As in the B/lines a single pair of flies was drawn at

random from the Kaduna population and mated in a vial. From their progeny a randomly drawn brother and sister were mated. From their progeny in turn another random brother-sister mating was made. Their progeny were allowed to multiply for five generations and the technique used was the same as applied to the B/lines.

As in the B/lines, the progeny of the fifth generation of expansion was used as the population to start the selection procedure, which was the same as in the two previous groups of lines. Five separate lines were started: A/1, A/2, A/3, A/4 and A/5.

4. The D/and E/lines.

These two groups of lines are treated together because, as it will be shown, they have a common origin.

The D lines were started from the fifth generation of expansion descended from the progeny of a single pair mating as done with the B/lines. However, instead of creating a single line a pair of lines were made: Two groups of 25 pairs were scored and within each group the ten highest scoring pairs were chosen as parents of the next generation of each line.

The E/lines were started in the same fashion as the A/ lines, one single mating followed by two full-sib matings and 5 generations of expansion. But the first pair of full-sibs was drawn from the progeny of the single mating which started the D/lines.

Similarly, a pair of lines was started from each original

line. Two groups of 25 flies were scored and again the highest scoring ten pairs were mass mated as parents of the next generation.

In doing so we produced pairs of lines related in origin not only within the same level of inbreeding but also between the two different levels.

Of each group three pairs of lines were made D/1A and D/1B, D/2A and D/2B, D/3A and D/3B and E/1A and E/1B, E/2A and E/2B, E/3A and E/3B.

The mating system and selection procedure was followed here as in the case of the A/, B/ and C/ groups of lines and maintained until it was considered that response ceased.

5. The F/, H/ and G/lines.

These lines were selected for low numbers of bristles and this is the only way in which they differ from the lines described above.

The F lines, of which three were made, F/1, F/2 and F/3, were started in the same way as the C/lines. 25 pairs chosen at random from the population cage were scored and the 10 pairs with the lowest count used as parents.

The H/lines were started in the fifth generation of expansion of the progeny of a single pair using the same technique as for the B/ and D/lines.

The procedure for deriving the G/lines was similar to that used for the A/ and E/lines. One single mating was followed by two full-sib matings, after which five generations of expansion

were allowed to take place before starting the selection procedure.

However, as in the case of the D/ and E/ lines each of the H/lines has a corresponding G/line because they were started from the same original single mating, whose progeny were ultised in the following way:-

One pair of full-sibs, randomly chosen were mated and in the sequence they became a G/line. The remainder of the progeny were put in a bottle and they originated one of the H/lines.

IV. RESULTS.

(a) The full-sib lines (Figures 2 and 3)

Owing to the genetic peculiarities of Drosophila this aspect of the experiment is perhaps best discussed in terms of the average of all lines. As is apparent from the graphs the rapid initial response was maintained for the first two or even three generations and this was followed by a slower rate of increase in bristle number. Response had ceased by the ninth generation although in some of the individual lines selection was continued until the twelfth generation.

It should be pointed out that no line had ceased to respond to selection before the fifth generation as was the case in Tantaway's (1959) experiment. Moreover, in some cases - lines $n^{o}8$, 14, 25a and 25b - the response was maintained until the 9th, 10th or 11th generation as can be seen from the graphs.

In every generation and in every line, after selecting the highest scoring pair in each of the three sub-lines, all the other 12 pairs were scored and mass-mated. This technique, without unduly affecting the precision of the results, allowed recuperation in any line which, as a result of low fertility, was in danger of extinction.

Line number 8 yielded a steady increase in sternopleural number until the 7th generation. Later, after failing twice through lack of fertility to produce an 8th generation, the line was kept without any further fertility problems until the 12th

generation when it was finally lost.

Line 14 showed a decline in mean number from the 1st to the 3rd generation and this was followed by a very marked increase until the 9th generation when it was entirely lost through infertility which extended also to the unselected mass-mated 12 pairs.

Lines 25a and 25b, related in origin as explained in the previous chapter, behaved in a remarkably similar manner and it can be seen that only after the 11th generation was there a cessation of response. This similarity of behaviour helps to invalidate any supposition of outside contamination of the lines to account for the protracted maintenance of response which was somewhat surprising in view of the level of inbreeding.

In analysing the variability of the lines, Fig.4, one is immediately aware of the consistancy in the level of the variance within lines and the marked increase of the variance between lines. Theoretical considerations and experimental evidence would allow this prediction.

The fact that the variance within lines remained constant in spite of the increasing level of inbreeding is a good indication of the additive nature of the genes controlling the character under selection. If recessive genes were important and if they occurred in low frequency the variance within lines would be expected to increase with inbreeding up to an F value of 50% and then to decrease on further inbreeding. Robertson (1952). As will be demonstrated when considering the problem of scale the variance within lines must, in fact, have been substantially reduced, an

observation which provides additional support to the theory that the genes controlling the character act additively.

A further point of note is the regularity with which the majority of the lines reaching a relatively high score either failed to leave any progeny at all or had their fertility grossly impaired. This phenomenon has been found by a number of other Drosophila workers. Mather and Harrison (1949) Clayton et al. (1957).

Lines derived from a single pair, and so related in origin, tended, in the main, to behave similarly in their pattern of response although lines 20/a and 20/b and 30/a and 30/b deviated markedly in this respect. However, in this latter pair in spite of the marked difference in score poor fertility was common to both members, a fact which was striking in the low scoring line, because decreased fertility was not a feature found in other low scoring lines.

Lines 18/a and 18/b which behaved similarly, were lost through infertility at generation 9. No progeny were obtained from either of the replicated sub-lines of each line or even from the mass-mated unselected 12 pairs.

(b) The mass-mated lines.

In describing the results obtained with these lines the order established in dealing with them in the previous chapter will be followed.

(1) The C/lines (Fig. 5)

The response to selection in these three lines was

maintained up to the 20th generation, but while in the C/1 and C/2 lines the rate of response declined after the 12th generation, the increase in C/3 was absolutely linear until the 20th generation when the line plateaued very suddenly.

The marked increase noted in C/1 and C/2 at generation 19 was possibly of an environmental nature. These two lines were discontinued after the 20th generation because they had inadvertantly been crossed.

The coefficients of variation for all the different lines are shown in Table 1. The sexes are treated separately. The trend in all the lines in both sexes was again quite uniform, and from an initial value around 10 - 11% in the beginning of the experiment the final values were around 6 - 9%. The coefficient of variation of the C/3 lines showed, in both sexes, an increase at the 12th and 13th generations for females and males respectively. This increase was accompanied by an increase in the rate of response to selection.

It is interesting to note that the unchecked increase in score of line C/3 occurred in spite of a decreasing coefficient of variation, especially after generation 14. In a simple model the approach to the plateau phase would be asymptotic through a slow and steady exhaustion of genetic variation. The other possibility would be a sudden cessation in response due to the establishment of an unstable equilibrium, with a greater or smaller amount of genetic variance still present. As already pointed out, maintenance of genetic variance in the plateau phase has been shown in Drosophila by Reeve and Robertson (1953)

and Clayton et al. (1957).

The genetic variance as measured by the coefficient of variation began to decrease after the 14th generation although there was no concomital reduction in the rate of response.

The establishment of the plateau was sudden at generation 20, although the genetic variance had already been much reduced and possibly exhausted (Table 1).

(2) The B/ and D/lines (Figures 6 and 8).

In the preceding chapter the origin of these lines was described and it was shown that in them, when the selection procedure started the level of inbreeding within each line was 25%. The expected scattering of the lines as a result of chance fixation, due to inbreeding can be seen in the graphs. But while the B/lines showed an increased average count of sternopleurals, which might lead one to conclude non-additivity of gene action, the D/lines showed exactly the opposite effect which by itself indicates how important a part is played by the environment and how needless it is to invoke the above mentioned genetic phenomenon.

In order to further clarify this point, the sternopleural counts made by Dr. Barry Latter on the offspring of single-mated 18 pairs of the Kaduna population, were analysed. The average sternopleural count of 17.35 in typical of the population whenever it has been examined for the character.

On considering the lines individually one is immediately aware of B/2 (Fig. 6).

This line not only showed, within the group, a greater

rate of response to selection and a higher final score than other lines within the B/group but also, during the course of selection, presented two very marked recessions. The first occurred at the 10th generation and was possibly due to contamination of the selected parents in the 9th generation. This, however, was of no great practical importance. At generation 9 the sternopleural count of this line averaged around 26. At generation 10 in both sexes some counts of 17, 18, 19 and 20 were found.

As selection was for increased numbers, the probability that there was an "outsider" amongst the parents of the 11th generation was very slight and the possibility was disregarded.

The second decline at generation 18 was certainly of an environmental nature, because it also occurred in other lines with a high score viz: lines C/1 and C/2, which were then at generation 6 after the accidental scoring referred to.

The observed variance in this line was somewhat erratic and although a decrease in the coefficient of variation occurred in the last generation this line retained some variability. After 12 generations of relaxation it was again scored and, as expected, the mean count had dropped from 32.74 to 24.40 with a coefficient of variation of 10.72% and 9.56% for females and males respectively.

Line B/3 also behaved in a somewhat unusual manner. After a regular increase in score amounting to a total of six bristles during the first 14 generations the count declined for 4 generations, and during this period the improvement achieved previously was halved.

The variability, however, remained almost unchanged. The occurrence of these two phenomena viz: the decline in score in

spite of selective pressure and the almost unchanged variability are striking and it would be of interest to conduct a detailed genetic analysis of the line. Unfortunately it has not as yet been possible to do this.

In the D/group the majority of the pairs of lines behaved with some degree of similarity. Only the lines of the first pair (D/1a and D/1b) showed a marked divergence which cannot be accounted for by sampling, although the behaviour up to the 10th generation can be accepted as being identical.

The 2nd pair of lines (D/2a and D2/b) can be said to have a similar pattern particularly if considered in terms of final score, although one member (D2/a) reached the plateau five generations sooner than the other.

The two lines of the third pair (D3/a and D3/b) showed an even more similar pattern of response.

In this group of lines the overall increase in score as the result of the selective pressure in the initial generation was quite remarkable and this was possibly due to the low scores obtained at the start of the experiment. This, in turn, was probably due to environmental influences.

The coefficient of variation was low in all the D/lines at the beginning of the experiment which was not at all the case in the B/lines.

The variability behaviour of all the D/lines, during the experiment, was very regular and the final values ranged from 5 to 8%.

(3) The A/ and E/lines (Figures 7 and 9)

At the start of the selective procedure these lines had a coefficient of inbreeding of 50%.

The most striking feature of some of them was the rapidity with which a selection limit was attained. In two of the lines, E/1a and E/1b, the score at the fourth generation was not different from the final score at the 15th generation. On the other hand, some of the lines continued to respond to selection up to the 20th generation.

In the A/group, line A/3 was lost in the 8th generation due to infertility. This line showed from the start the presence of the gene hairy, and the flies selected in each generation were, presumably, heterozygotes for this gene. The flies which were phenotypically hairy, were deliberately avoided, but the descrimination was not effective against heterozygotes. This may account for the reproductive failure in the 8th generation.

In the E/lines the almost identical behaviour of the lines within pairs is again quite easily seen in two of the pairs (E/1a and E/1b, E/2a and E/2b) but a marked divergence is noted in the other pair - E/3a and E/3b. However, this pair, like the other two showed a similar pattern of decrease in the coefficient of variation, with the progress of selection.

As explained in the previous chapter the D/ and E/lines were related in origin and each group consisted of 3 pairs of replicated lines.

Fig. 8 and Fig. 9 show those two groups and it can be seen that some of the replicated pairs, related in origin either

within or between groups, behave identically while in other cases, the two members of a pair or the two pairs of common origin behave quite differently.

(4) The F/lines. (Fig. 10).

The response to selection for decreased bristle number, although less marked than when selecting for increased number of sternopleurals, was maintained up to the 22nd generation.

As with the C/lines, an order was soon established amongst the F/lines which was almost perfectly maintained during the whole experiment, a pattern which is in agreement with the observations made by Clayton et al. (1957) and which is quite easily verified in all the groups of lines produced in this experiment.

All the lines of this group show a reduction in variability which, in terms of the coefficient of variation, is of the order of 20%, Table 1. It can be seen that the variability of the lines, decreased regularly. In line F/3, except for a few minor overlaps, the males are consistently rather more variable than the females.

(5) The H/lines. (Fig. 11).

At the start of the selective procedure all the H/lines had an inbreeding coefficient of 25%. The scattering of the lines about the mean value was found as expected. As in the case of the A/ and B/ lines the mean value is higher than in the base population.

An average response was maintained up to the 14th generation. Table 1 shows the coefficients of variation of all the lines. It can be seen that within each line the males are more variable than

the females, a phenomenon which is particularly noticeable in lines H/1 and H/5.

(6) The G/lines (Fig. 12).

The scattering of the lines as a consequence of the level of inbreeding F = 50%) is very marked and again an increase in average score was found.

The response to selection is a common feature of all the lines although, as expected, some have a more marked response than others.

Although some of the lines do occasionally overlap, the general ranking is obvious.

The H/ and G/ lines, as explained, are related in origin. It cannot be said that the behaviour of the pairs is very similar. However, in no case did a G/line reach a better score than an H/line, a fact which falls within the expectations.

As in the H/lines there is a suggestion of rather more variation among males than females although in no case is it as marked as in the H/1 or H/5 lines.

Bridges and Brehme (1944) have shown that in the X chromosome of Drosophila there are at least 9 different loci occupied by genes with a recessive allele, which decrease or in some way affect bristles. It is possible that the effects of the segregation of such alleles in the male may provide an explanation for the observed greater variability.

In none of the lines selected for increased numbers of

sternopleurals was there a similar suggestion. Neither the males nor the females seem to be more variable.

Table 1 shows the coefficient of variation for all the lines. The sexes are treated separately, because, with very few exceptions, the sex difference was marked and constant.

Table 2 shows the ratio of female to male score at five generation intervals.

Table 3 shows the realised heritabilities of all the lines. For each line the overall heritability as well as the heritabilities for successive periods of five generations each, were estimated.

V. SCALE.

(a) Genetic variation.

In Fig. 14 the average response to selection of all the groups of mass-mated lines is plotted. The degree of asymmetry is so marked that it was decided to plot the same values on a log scale, Fig. 15. In so doing we found that we had in fact produced a greater change in the upward direction than in the downward and in terms of final response the degree of asymmetry is much less marked than on the arithmetic scale. The remaining asymmetry in the log scale is perhaps a reflection of different frequencies of the genes responsible for the change under selection.

The results, apart from anything else, show the inadequacy of the arithmatic scale in representing the genetic progress achieved by selection. Furthermore we must bear in mind Mather's (1949) warning to the effect that "the replacement of A for a or B for b in any genotype and under any set of environmental conditions should make the same difference, no matter what the measurement associated with the original genotype and conditions might be". It was therefore decided to try to measure the effect of a given gene substitution on differing genetic backgrounds. This was possible by virtue of the fact that the bristle character is almost entirely under additive genetic control. Clayton et al. (1957), the heterozygotes being approximately intermediate and there being no evidence of epistasis.

To achieve this aim two ways were open. The first, to cross a visible dominant gene with an effect on the character into different long selected lines.

This technique, however, doesn't stand up to a critical judgement, because the comparison of the effects of segregation in different background is only valid if the alternative allele to the dominant marker gene is the same in all different backgrounds. And this is certainly not the case.

The second, making use of the absence of crossing-over in Drosophila males, is to compare, instead of the effect of a single gene, the effects of two chromosomes upon the mean of the character in different genetical complements, i.e. when the other chromosomes are varied.

To do this the dominant gene "hairless" was crossed into a low line (LF_4) which had ceased to respond to selection for decreased number of sternopleurals. By repeated back-crossing, using the low-line males on the heterozygote for "hairless" females (the homozygote hairless is inviable) the dominant marker gene was gradually built up on the background of the low-line third chromosome. After 10 generations of back-crossing, heterozygote males were mated to females of the highest sternopleural line that we had available (C/3 A/5). From the progeny of this cross, hairless males were collected. The third chromosome of these males came one from the very high-line and the other from the low-line into which they had been back-crossed, i.e. the gene "hairless" which itself depresses sternopleural bristle count. Because there is no crossing-over in the males these two chromosomes will then

segregate as units. The presence of the marker gene (absence of the post-vertical bristles and interruption of the 5th longitudinal wing vein) allows the measurement of the effects of this chromosomal substitution in any background by crossing the males to different selected lines.

The segregating males (their 3rd chromsome being one C/3 A/5 and the other Lf4/H where crossed to four different lines. Two of them being the two extreme lines (C/3 A/5 and Lf4), the remaining ones having no genetical connection with the two lines constituting the cross except that they came from the same base population.

The results are shown in the following table, in which the mean scores for wild type and hairless flies are given for the whole series of crosses done.

Cross	Hairless	wild type	$\frac{H/-6}{+/-6}$	
$(C/3 \times A/5)/H_L \times F/1$	12.17	17.62	.53	11.5
" $\times H_2$	13.55	20.78	.51	13.5
" $\times H_{F4}$	17.69	32.29	.44	31
" $\times (C/3 \times A/5)$	24.54	47.50	.45	50
" $\times LF_4$	11.58	17.26	.50	11
x $\times H/_4$	14.49	23.01	.50	16

Any experimenter with Drosophila familiar with sternopleurals is aware of the existence of two different groups within the area occupied by these bristles. Three of them, on either side, usually

the more dorsally situated, are almost invariant to selection pressure especially when selection aims at decreased numbers. For that reason the actual counts obtained in scoring the wild types and hairless flies have been reduced by six. It can be seen that after the subtraction of the six invariant bristles the effect of the chromosomal change, is the same or almost the same in all the crosses. The effect of the low "hairless" chromosome compared with the high scoring third chromosome is to reduce the number of bristles by a factor just below one half.

The constancy of the proportional effect of a given genetic substitution in different backgrounds is good and clear evidence that the correct scale for the consideration of genetic variance is the logarithmic one.

It should be emphasised that there is no evidence of interaction between genes at different loci. But this constancy of proportional effect of a given genetic substitution in different backgrounds is no more than a regular pattern of interaction. However, it seems that this form of interaction is only important when there is a wide range of variability and again only in that situation it is possible to investigate it.

(b) Non-genetic variation.

During the whole of the experiment the left and right sides of each fly scored were separately recorded. In this way and as a by-product of the experiment, we had available data pertaining to bilateral asymmetry of sternopleural bristles of 46 different lines. The range of bristle count between the lines

extends from 10.5 to 52.4.

The measure of asymmetry used was the mean square difference between left and right sides, $V = (L - R)^2/n$ as defined by Mather (1953) (where n = number of flies) or Av (d^2) in the nomenclature of Reeve (1960) or σ^2_p, the variance of the difference following Clayton et al (1957).

In order to increase the accuracy of measurement the within line data of the last four generations were pooled. In this way the number of flies contributing to the determination of each point, for the two sets of lines (i.e. full-sibs and mass-mated), were 60 and 100 respectively. The sexes were treated separately.

The points obtained for each line and the corresponding level for total count can be seen in Fig. 16, which also shows the calculated regression lines. These latter calculations are based on the assumption that there is a linear relationship between the variance of the difference and mean and not with the square of the mean. This aspect will be discussed later.

The deviation of each individual point from the corresponding regression line was calculated, in order to test whether there was any tendency to increased or decreased asymmetry within the generations or the lines. Bearing in mind, the differential breeding systems used during the selection process, the two sets of lines were analysed separately. The analysis was done for both sexes. The results are given in the following table.

(a) Full sib-lines males

Between generations	3	1.495	0.498
Between lines	32	48.764	1.523
Residual	96	131.718	1.372
Total	131	181.977	

(b) Mass-mated lines, males

Between generations	3	3.168	1.056
Between lines	12	10.466	0.872
Residual	36	18.113	0.503
Total	51	31.747	

(a) Full sib lines, females

Between generations	3	8.121	2.707
Between lines	32	40.514	1.266
Residual	96	110.676	1.153
Total	131	159.309	

(b) Mass-mated lines, females

Between generations	3	1.353	0.451
Between lines	12	7.347	0.612
Residual	36	45.090	1.252
Total	51	53.790	

To check whether there was any consistent positive or negative deviation between lines the average deviatinns of both sexes for each line were added.

The analysis of these data did not reveal any trend, as can be seen in the following table.

(a) Full-sib lines.

	D.f.	S.S.	M.S.
Between line	32	48.512	1.516
Line sex interaction	32	49.394	1.543

(b) Mass mated lines.

Between Line	12	4.697	0.391
Line sex interaction	12	6.942	0.578

The data pertaining to the selection experiments with sternital bristles done by Drs. Clayton, Morris and Robertson were made available to us.

The same method was applied and the results are presented in Fig. 17.

On this evidence it can be said that the variation of sternopleural counts between sides of the fly or the variation of sternital count between adjacent segments clearly follows the law of proportionality to the mean number of effective bristles, and theoretically it can be assumed that this is the expectation.

There is good evidence presented by Reeve and Robertson (1954) and Clayton, Morris and Robertson (1957) that the non-genetic variation both of sternital and of sternopleural bristles

is not truly environmental in origin in the sense that it does arise from the effect of an external environment on the individual animals. Almost all the non-genetic variation observed in a random breeding population can be accounted for as differences between adjacent sternites or between the two sides of the fly.

The variation is then specific to the individual sternite or to the individual side of the fly and can be considered as due to some kind of error of development. This variance has been given several names: chance of stochastic variability, Reeve and Robertson (1953), developmental error, Clayton et al (1957) and by analogy with electronic jargon, "developmental noise" Waddington, Graber and Wolf (1957).

Is there any a priori reason to choose one particular scale rather than another in dealing with this type of variability?

We would point out in this context that we are dealing with the counting of individual objects and not measurements of some metric character. The variability in bristle counts between sternites can then be considered as due to two factors. First, at a molecular level, differences between sternites in the concentration of bristle-producing substance (whatever that may be) and secondly on the regularity of the pattern of the bristles produced. It is this latter aspect of the question that we wish particularly to emphasise. Let us suppose that in the adjacent sternites the concentrations of bristle-producing substances are the same, that bristles are equally likely to be produced at any point in the available surface, and finally that there is no

interference between them, that is to say that bristles are scattered at random over the available surface. In this situation we would then expect that the distribution of number of bristles per sternite or per side would be Poisson, and that, if our index of variability was the squared difference between adjacent sternites, or between both sides, we should then find that the variance of the difference was equal to the sum of the bristle counts on the two sternites or both sides. But, in fact there is interference between the bristles (sternitals or sternopleurals) and we do not find that they will occur very close to each other. If the pattern of bristles was extremely regular we should then expect to find little or no variation in bristle counts. An example of this is of course given by the major scutellar bristles which have a perfectly regular distribution on the scutellum. But what of the intermediate case where there is some interference between bristles. It is extremely difficult to give a theoretical discussion of this situation in two or three dimensions, but the problem has been discussed in one dimension by Owen (1949) in treating genetical interference. He was then dealing with the problem of the distribution of chiasmata in a given length of chromosome and was defining the problem in terms of the distribution of the distance between crossover points on a chromatid. He was able to show that in this situation the variance of the number of chiasmata in a given length of chromosome would be proportional to the average number in that segment, and that the constant connecting the two would be the squared coefficient of variation of the distance between adjacent crossover points.

Here we have a precise re-statement of what was said earlier. If there is no interference between crossover points and the chance of occurrence of the subsequent crossover is independent of the distance from the previous one, then it can be shown that the variance of the distance between adjacent crossover points is equal to the square of the mean distance and this is the situation in which we expect to find a Poisson distribution. On the other hand, if the distances between crossover points are always exactly the same we shall expect to find no variance of the number of points in a given segment. It is extremely difficult to extend these results into two dimensions. It can, however, be seen qualitatively that some law like this must apply in order to satisfy the rule of the additiveness of variance of the number of points in two adjacent areas. What we then mean by regularity of a pattern will be measured as the shape of the distribution of the distance from a bristle to its nearest neighbours. The average number of bristles in the area will then be dependent on the average distance to nearest neighbours, and we should expect selection to have an effect on this and not necessarily on the shape of the distribution curve. Thus, if non-genetic variation is all of this kind we should expect that the mean squared difference between the sternopleural counts on the two sides of the fly should be a constant multiple of the mean count. But, in the case of sternopleurals however, we must take into account the observed fact, already mentioned, that three of the bristles on either side of the fly are different in kind from the others, so that

the effective mean from our present point of view will be the actual mean minus 6. To the extent that difference between segments or between sides of the fly are actually due to differences in the concentration of bristle-producing substance or perhaps to differences in the area on which the bristles may be formed one might expect that the variance due to these causes would increase as the square of the mean number of effective bristles.

Experimentally the problem is not easy to tackle because if one alters the mean of the population one might expect from some points of view to be affecting the degree of variability. For instance, if there are genes controlling variability then we may expect by selection of the extremes of the population to increase the frequency of these genes, and therefore to increase the inherent variability.

Bearing in mind the possibility that the selection may increase this variability we can, however, from the data presented, Fig. 16 and 17, accept the existence of the strong proportionality of mean and variation of the difference. In the initial population in which the number of effective bristles (mean - 6) concerned was 11 the mean square difference of the two sides was close to 1.8. In the very high selected line with an effective number close to 47, an increase by a factor of 4.4, and the mean square difference found is very close to 7.5. This is very close to what we would expect if the variance was proportional to the mean and certainly very strong evidence against the variance being proportional to the square of the mean. If this was the case the expected variance

in the high lines would be around 36 units, which it quite certainly is not. The lowest point found, corresponding to the lowest line produced, in which the mean over the past few generations was just below 5 effective bristles, was of the order of 0.8.

The evidence available from the sternital counts (Fig. 17) is at least as strong although there was an apparent change in the situation in all the down selected lines in that once their mean had passed below a certain critical value the variation suddenly increased greatly. However, provided we remain above this critical value (below 15) again we find a clear proportionality between total count and the variance of the difference between segments.

Two facts should be pointed out. First, this critical value, below which this proportionality of mean and variance breaks down is parallel with morphological disruption of the flies as reported by Clayton et al (1957). Secondly, it is interesting that the proportionality constant is the same in the case of sternopleurals and sternitals, provided, with those we remain above the critical point. This is presumably a reflection of a similar regularity of pattern in the case of the two sets of bristles. And although no apparent connection exists between bristle pattern and ovarioles, it is whorth while to quote Reeve (1950) "we may note in passing the curious fact that sternites with twenty chaetae and ovaries with twenty ovarioles show almost the same variance due to chance effects, but whether this reflects any fundamental similarity in the casual factors underlying the variation it is not easy to decide.

The evidence presented, both practical and theoretical, does suggest that in considering Drosophila bristle counts, abdominal and sternopleural, the correct scale for the discussion of genetic phenomena is not the correct scale for the discussion of the non-genetic variation. And this fact is a confirmation of Mather's (1949) prediction that it may be impossible to find a scale which will adequately make additive the variation due to genetic and non-genetic causes.

This fact is perhaps the justification to a somewhat puzzling situation found when comparing the results obtained in selecting for bristle number, in both directions. The heritability tends to increase in the early generations of selection to increased numbers and to decrease when selecting downwards. The different scallar effects on genetic and non-genetic variation may be the cause of this. If we select upwards the effects of the genetic segregation will be increased to a proportionately greater extent than will the non-genetic variation and the heritability will increase, and the reverse will apply to selection downwards.

Fig. 13 shows the realised heritabilities of C and F groups of lines. By plotting bristle number against the cumulative selection differential it is possible to visualise in any line at any generation the realised heritability as shown by Falconer (1953). As pointed out and in the initial generations the trend in the down selected lines is in the direction of diminuition and inversely for the lines selected for increased numbers.

VI. DISCUSSION

The method followed in the presentation of the results was to point out, discuss and,whenever possible, interpret, at the level of single lines. Here we shall make a broader survey of the main findings and if possible generalise at the level of the aims for which the experiment was designed.

Bearing in mind the assumptions put forward in the introduction it can be said that the results are in relatively close agreement with expectation.

In consdering the inbred lines it is a temptation to try to determine what part of the divergence between lines was due to drift, Wright (1931), and what part was played by mechanisms of drift-reinforcement, Waddington (1957). The concept of drift, postulates chance fluctuations in gene frequencies, leading in some cases to chance fixation or elimination of genes, through random elimination of gametes.

The variance due to drift for a single gene has been given by Wright (1931) as

$$\sigma_g^2 = q\,(1 - q)/2N$$

Wright (1951) has also indicated that if the system of mating is one of subdivision into strains (or lines) with internal random mating then the average variance within them, that is the additive genetic variance, falls off by the proportion of F, the cofficient of inbreeding becoming $(1-F)\ \sigma_G^2$, and the variance between such strains becomes $2F\ \sigma_G^2$.

Thus the variance between lines can be taken as an estimate of the amount of drift variance providing it can be assumed that there are no environmental effects peculiar to one line and not to another. This variance component "between lines" could be calculated for any given generation and equated to $2F\sigma_G^2$.

This would provide a value for F, on the basis of data obtained in a randomly propagated series of lines. Although this coefficient of inbreeding can be calculated by the use of the formula given by Wright (1931)

$$\frac{1}{8M} + \frac{1}{8F}$$

where M and F are the actual numbers of males and females, the differential reproduction ability of the parents is not accounted for by the formula, and the result is not necessarily true. For Drosophila, Crow (1954) has shown unequal abilities of egg-laying and mating for females and males respectively. He found, in Drosophila experiments that the ratio of the effective number to the actual number is 0.71 for females and 0.48 for males.

However, for other species if the drift variance could be estimated with reasonable accuracy, then it would be possible to have an estimate of the amount of inbreeding actually produced during the process of line derivation. From the F value so calculated an estimate of the effective number of parents in the lines would become possible.

From the data collected during the experiment involving the full-sib lines it is possible to calculate the expected drift

variance at any generation and to compare it with the observed data. The difference between them would represent the effect of selection in reinforcing the natural drift occurring during the propagation of the lines. These results are given below, for both sexes at generation 3 and 10.

	♀		♂	
Generation	3	10	3	10
Expected drift values	1.705	2.958	1.733	3.015
Observed values	4.237	7.843	3.255	6.020

We were rather fortunate to have available the data for full-sib lines produced by Dr. Barry Latter, as mentioned in the results. He produced 18 full-sib lines which were propagated on an entirely random process. At the third generation with an F value of .5 the value found for the component of variance between lines and pooling the sexes was 1.69. This figure is in remarkable agreement with the theoretical expectation and so it is legitimate to assume that the difference between the observed and expected values in the above table provide a good indication of the effectiveness of selection in reinforcing the natural drift produced by sampling and enlarged by the random-elimination or fixation of genes from one generation to the next.

In discussing the mass-mated we shall concentrate our attention on the effects of restriction on the population size on average response on the ultimate limit and the asymmetry of response.

Whether the average response to selection is appreciated in Fig. 14 which is an arithmetic scale or in Fig. 15 which is a logarithmic one, it can be seen that the observed responses (up to the 5th or 7th generations are, in terms of between group comparisons, in close agreement with expectation.

In the down selected lines the agreement maintained for a larger number of generations. It can be said that the agreement at the end of the selective procedure in thos lines is fairly good.

The calculation of the expected response to selection is based on the following formula:

$$= \bar{I}\, h^2\, \sigma_p\, (1 - F)$$

in which $\bar{I}$ is the intensity of selection in standard deviations, σ_p the standard phenotypic deviations, h^2 the heritability of the character and F the coefficient of inbreeding.

Lines of groups C and F, starting from the base population are assumed to have an F value equal to zero. Lines of groups B and D in the up selected lines and group H lines in the down selection having passed through a single-mating during the creation of the lines have an F value of 25%. The lines of groups A, E and G, however, having passed through a single mating followed by two full-sib matings had, at the start of the experiment, an F value of 50%.

Although as previously pointed out, the agreement between observation and expectation in terms of level of response is close up to the 7th generation in the high lines and up to at least the

12th generation in the low lines, it is nevertheless of interest to consider the situation in terms of a time scale, i.e. what is the effect of the bottlenecks in reducing the numbers of generations to reach the limit?

Robertson (1960) has shown that the number of generations to reach the limit, or the time scale, is directly proportional to N (the effective population size). As such, this question is not answerable until some effective method of determining the number of genes affecting the character under selection and their respective gene frequencies is found. Even then, linkage problems pleiotropic effects and interactions will be a source of interference with any simple model or theory.

And the question not only is not answerable but also lacks meaning, at least in considering the practical applications. The approach to the limit is asymptotic and so is perhaps more useful to ask what are the effects of the bottlenecks in reducing the time taken by the mean gene frequencies in reaching half-way to the limit. Robertson (op. cit) using a physics analogy has put the question "what is the half-life of the selection process?" and has shown that with low values of NS (N being the effective size and S the selective advantage) the half-life will probably by between N and 2N generations. And further he showed that if the half-life of a selection programme is reached well before the range of N to 2N, expected when the chance of fixation is not high, it is possible to assume that all desirable alleles have been fixed.

From Figs. 14 and 15 it is possible to ascertain the number

of generations required on average, by each group of lines to reach $^{3}/_{4}$ of the total progress made. It took 13 generations to the 3 lines of Group C to make $^{3}/_{4}$ of the way, 9 generations to the 11 lines of groups B and D and 8 - 9 generations to the 11 lines of groups A and E. In the down selected lines the picture is almost identical. It took 11 - 12 generations to the lines of group F to make $^{3}/_{4}$ of the total progress and around 9 generations to the lines of groups H and G to reach the same point in their response. This identity of effect of 1 or 3 restrictions in the time scale of the selective process is also present although not so markedly in terms of level of response. This in fact is the expectation. As pointed out in the introduction the first restrictive mating is the most powerful agent in effecting gene frequency changes or genetic changes by loss. And the lower the initial gene frequency, the greater will be the chance for a gene to be lost from the population size by a reduction in size (Robertson 1960). The extent to which the selection limit will be affected by varying degrees of population restrictions and by varying initial gene frequency is discussed theoretically.

Since in the present experiment we have no direct information concerning either the effective number of genes involved or their frequencies, the material is not ideally suited for a critical test of these hypotheses. Nevertheless a comparison of the selection limit of the D/ and A/groups of lines (which were subjected to 1 and 3 restrictive matings respectively) and a comparison (which is possibly more valid) of the paired lines of groups D/; E/ and H/; G/ give the impression that the frequencies of the genes involved

are low. The differential effects of one and three restrictions were small in all the lines which were paired in origin. A similar tentative conclusion can be drawn from a comparison of the selection limits encountered when no restriction and one are imposed. If, according to Robertson (op. cit) the gene frequency lies between .3 and .5 a single restriction of parents to one pair reduces the potential subsequent improvement to 50% of the obtainable from the base population. In Figs. 14 and 15 it can be seen that the average response of the lines on which a single pair restriction was imposed is half that of the unrestricted lines.

In the presentation of the results an analysis of the variability of the full sib-lines (Fig. 4) showed that the genetic component of variance within lines (σ^2_w) apparently remained constant in the females and decreased slightly in the males. However the application of a suitable scale transformation show that the mean square difference between left and right sternepleural counts (σ^2_D) is directly proportional to total count. As such it is perhaps legitimate to suggest that σ^2_w was in fact reduced.

In the following table the values for mean count, σ^2_w and σ^2_D for the original and 10th generations are given.

	Mean count		σ^2_w		σ^2_D	
generation	♀	♂	♀	♂	♀	♂
0	17.66	17.17	3.5	4.5	1.278	1.782
10	23.706	22.825	3.65	3.8	3.401	2.417

Although the evidence given in the chapter dealing with scale suggest that the appropriate scales for genetic and phenotypic

values are not the same, the temptation to make a straight comparison of the values of σ_W^2 and σ_D^2 at the two levels (generation 0 and 10) is rather strong. It has been shown Clayton et al. (1957) that σ_D^2 makes up for almost all the non-genetic variation observed in analysing sternopleural or abdominal bristles of a random-breeding population of Drosophila, and accepting this fact the obvious conclusion is that the genetic component of variance within lines (σ_W^2) did decrease with the progress of the selective procedure. In fact if the comparison can be made it is possible to say that in the females all the genetic variability within lines was exhausted. In the males although the comparison would give an indication of a substantial reduction (around 50% of the original value) the conclusion points again to the larger variability of the males, which as said in the "Results" it is perhaps a reflection of the buffering of the females afforded by the presence of two X chromosomes as opposed to the hemyzygotic condition of the males.

Before any generalization is attempted or any practical conclusion drawn, the low repeatability of the replicated lines should be emphasised. Soon after the start of the selective procedure the lines showed an individuality which is reflected in the pattern of response in variation, ratio of female to male score and in some cases by the possible presence of lethal genes. The presence of lethal genes was suggested either by infertility or by a plateau phase in conjunction with a high residual variability.

The small number of chromosomes and the absence of crossing-

over in the male are strong causes of inflation of the divergence and lack of repeatability of the lines reported in this experiment. It is not easy to allocate the observed divergence into the causes specific to the genetic constitution of Drosophila and the more general possibility of multiple allelism. This difficulty does not in any way lessen the need of an experimental approach to the problem which arose in interpreting the results obtained, and which essentially is the not new but basic question of how to properly sample a base population.

The comparison of the results obtained in the full-sib lines with the ones of the mass-mated lines suggest that a useful approach would be to create a very large number of small lines to select the best, cross them, and from the progeny obtained restart the process over and over again. In Fig. 4 the variance components obtained from analysing the variability of the full-sib lines are plotted. It can be seen that the component of variance between lines reached a maximal value at the sixth generation. On the other hand the response to selection of the same lines Fig. 2 and Fig. 3 show that by the third generation the divergence is already marked. Considerations of time-saving would advocate the crossing of the lines chosen to be maintained in the process of building up the useful genetic material at that third generation. Dealing with sternopleurals, where at least 80% of all the genetic variance is additive one would be entitled to disregard the lines with the worst performance and to use only the best ones. In sternopleurals there is no suggestion of special combining ability, Bell et al 1955.

In considering the crossing of the selected lines two ways are possible. To make a deallelic cross, including the reciprocals, or else to mate at random representatives of all the selected lines, allow for one or two generations of expansion with random-mating and restart the selective process from the new gene pool so formed, and so on. In short a funnel-like operation to bring together all the useful genes.

From a series of crosses of the highest-scoring mass-mated lines developed during the experiment, Lines C/3, B/2 and A/5, we have evidence that the average number of sternopleural bristles of both sexes can be increased to 52. Some females were found with a score of 61 bristles. In terms of standard deviations the average bristle number of the base population was increased by 20.64. No further crosses were made in order to test whether this could could be further increased or whether it was a reflection of a physiological limit. The indication afforded by the smallness of the coefficient of variation of the line with the average of 52 bristles points to a limit evolved by exhaustion of genetic variation. This aspect will have to be tested. However, a limit or not, it is a target which through mass-mating was reached after 40 generations of selection. How many generations will it take to reach the same point using the programme of sub-division into a large number of small lines and crossing?

This is a practical question which can be tested by considering for instance line number 9, Fig. 2, which is a full sib line, and C/3, Fig. 5, which is a mass-mated line. The first reached the count of

27 sternopleural bristles by the second generation - an increase of 10 bristles in two generations, and after another 4 generations plateaued at a count of around 30. Line C/3 reached a count of 27 only after the 8th generation, but the response to selection was maintained up to the 20th generation and at that time the average count was 43 bristles.

Would it have been possible to increase the available genetic variability by crossing line number 9 with some other line and thereby raise the selection limit?

To what extent could the process be advantageously repeated or, conversely, where would the reconstitution of genetic variability by crossing (for realising a subsequent selection response) cease to be effective? The limiting case would be when there is homozygosity both within and between lines but it is highly unlikely that such a situation would occur between replicates of selected lines unless a very severe bottleneck was imposed at the outset, an eventuality of doubtful practical probability.

Although Drosophila physiology is very far removed from that of domestic animals there is no reason to suppose that the genetic mechanisms are markedly different and so an extrapolation is perhaps legitimate. In commercial poultry breeding it is already an established practice to create a large number of lines, the number depending on the facilities available, and to test them for some desirable characters. This subdivision and crossing is the basis of selection programmes aimed at the improvement of crossing ability.

How efficient would be a funnel-like operation in sampling an unselected population of domestic animals? It is possible that this is a problem of more than just academic interest. It is legitimate to assume that the sampling of unselected populations of domestic animals or unimproved varieties of cultivated plants can yield genes which could be advantageously used. In the symposium in statistical genetics and plant breeding held in Raleigh, North Carolina, the idea of testing for the existence of useful genes in wild varieties of Andean maize and to cross them into highly selected strains was suggested, Comstock (private communication by Dr. Alan Robertson).

However the reservation must be made that this approach is not intended to be of general use. It will perhaps be useful when dealing with characters on the high side of the heritability spectrum. Characters which through the evolutionary history of the species have been in some way connected with fitness and for that reason are in the extreme low side of the heritability spectrum are quite unresponsive to selective pressures, since developmental buffering will conceal a greater part of the gene-activity, Waddington (1950). In these circumstances it was suggested, Waddington (op. cit) that a useful approach would be to break down the buffering system either by a powerful environmental influence or else by the introduction, into the stock to be selected, of some genes not characteristic of the original wild population. The idea is to de-stabilize the developmental pathways so that the resulting end-products are more variable in many different characters.

SUMMARY AND CONCLUSIONS

An attempt has been made to experimentally investigate the effects of restriction on the population size on the ultimate limit of selection through chance fixation.

The characters used for this study was the number of sternopleural bristles of Drosophila melanogaster.

The investigation was sub-divided in two main parts, viz, full-sib mating and selection and mass-mating of selected lines.

The full-sib lines numbering 33 were all submitted to the same mating and selective procedure. Within each line, five pairs were scored and the best pair was allowed to mate. On average, the selective procedure lasted, for each line, for 10 generations.

In the mass-mated lines and in order to measure the effects of restriction on the population size, three different values of F (the coefficient of inbreeding) were created (no inbreeding, 25% and 50%). From each of these points a number of lines were started.

6 from the base population, without inbreeding, 3 selected for increased numbers and 3 in the reversed direction. 16 with an F value of 25%, 11 for increased numbers and 5 in the reversed direction. 16 with an F value of 50%, 11 for increased numbers and 5 in the reversed direction.

In all these lines, the mating system and the selective procedure was the same. Within each line 25 pairs were scored, and the 10 pairs with the best count in the direction of selection were mated.

It has been found, at least in experimenting with Drosophila, that the effect of chance fixation needs to be accounted for.

From the results obtained in selecting the different groups of mass-mated lines and in comparing their average responses two main implications were gathered.

1. The effective genes must have a frequency of around 3 or 4.

2. The effect of the first restrictive mating or bottleneck is by far the more important in affecting the subsequent reponse to selection. 50% of the possible response of the base population is lost when a restriction to a single pair was made.

By analysing the data of left and right counts of sternopleurals it was found that the bilateral asymmetry is a direct function of total count. On the other hand, a genetic substitution in different backgrounds revealed a constancy of proportional effect. These two facts indicate that the scales for consideration of genetic and non-genetic phenomena, are not the same.

It is suggested that a funnel-like operation of sub-division in small-lines and crossing, is a good approach to the genetic sampling of an unselected population and that it can be used as a tool to promote a more rapid improvement, at least in such characters as those with a high heritability.

TABLE 1

Coefficients of Variation.

Lines	C/1		C/2		C/3		B/1		B/2		B/3		B/4		B/5	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Gen. 0	9.3%	12.7	9.9	9.0	9.2	11.6	10.9	10.0	8.2	10.4	10.9	13.3	10.9	11.9	11.4	10.7
1	9.5	7.5	10.4	12.0	11.1	9.6	10.7	8.5	8.4	9.9	9.0	14.5	9.6	11.6	7.2	11.4
2	9.5	10.7	12.4	8.4	12.4	12.8	10.7	9.6	7.8	13.6	14.3	12.9	9.9	11.0	8.7	8.5
3	12.2	11.0	10.4	8.8	10.4	9.7	6.3	9.9	8.6	11.7	11.4	10.2	12.7	11.1	8.2	7.8
4	10.7	10.8	12.5	13.5	10.7	10.5	9.0	10.9	13.1	14.4	14.5	12.0	12.4	8.9	8.7	9.1
5	7.8	9.4	9.9	11.4	10.1	10.3	10.1	9.5	6.6	9.6	10.5	12.3	9.2	7.6	11.3	9.3
6	9.2	8.1	10.5	11.1	12.0	8.5	10.6	11.3	10.8	11.9	11.2	11.8	12.2	8.2	6.5	13.4
7	11.3	10.2	12.0	9.9	11.7	10.7	9.5	8.1	11.6	10.1	9.1	9.5	8.4	6.9	7.8	8.3
8	10.9	10.9	11.8	9.4	10.1	14.3	12.6	12.6	12.6	8.6	10.5	13.5	7.1	8.2	8.8	8.0
9	10.1	7.9	12.6	9.2	9.2	7.9	10.3	9.9	10.2	9.8	10.3	12.2	8.9	8.0	5.7	6.7
10	6.1	9.7	10.6	9.9	9.7	13.4	9.4	5.7	18.2	14.3	12.7	13.9	6.2	13.0	10.2	8.1
11	7.9	9.5	11.4	11.2	9.2	10.9	6.9	8.1	12.2	11.3	11.7	10.2	8.5	8.3	9.3	7.8
12	8.3	8.1	9.3	9.1	11.3	13.1	8.5	8.7	11.7	8.9	11.4	10.2	9.8	7.7	6.9	6.6
13	7.2	7.8	7.5	8.4	10.8	14.4	9.9	7.7	10.8	9.8	11.7	9.8	6.8	11.1	8.2	6.6
14	8.3	8.4	9.3	9.6	7.0	11.5	6.9	10.9	8.8	7.5	11.6	9.9	8.0	7.0	6.8	8.2
15	5.2	6.8	10.2	7.0	6.9	9.9	8.9	6.9	8.0	10.4	9.0	10.9	8.0	8.9	8.1	6.8
16	6.2	9.1	7.4	7.3	8.4	8.6	10.4	9.2	10.8	8.7	7.8	12.8	9.6	8.8	7.1	7.2
17	7.1	8.3	7.6	7.9	9.9	6.3	7.3	8.3	11.3	8.9	12.3	7.5	6.2	9.1	6.0	5.8
18	5.9	8.6	9.7	6.8	5.9	5.2	9.3	7.1	7.9	7.5	8.8	9.5	9.5	8.9	8.3	7.8
19	9.4	6.6	7.9	10.0	7.0	7.8			8.7	8.5	11.1	9.7				
20	10.9	6.1	9.1	8.4	6.7	6.5			10.2	9.3						
21					6.6	6.2			10.9	10.4						
22					7.0	6.9			8.4	7.0						
23					6.6	9.1										
24					7.8	5.6										
25					7.6	7.3										

TABLE 1 (continued)

Coefficients of Variation.

A/1		A/2		A/3		A/4		A/5		D/1a		D/1b		D/2a		D/2b		D/3a	
♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
13.0	9.5	11.4	11.2	8.3	11.9	12.4	10.7	10.0	13.1	8.9	7.5	7.7	9.5	6.9	7.0	6.7	8.2	8.3	9.3
14.3	9.5	8.1	9.9	12.0	10.3	9.9	9.7	12.5	13.6	9.3	8.7	10.2	10.3	11.2	8.4	9.2	10.0	11.3	10.9
10.7	13.4	9.9	8.8	9.3	9.2	11.5	7.2	9.2	9.3	10.1	11.5	9.3	9.9	10.9	10.2	8.9	9.7	9.9	10.3
10.0	14.6	7.8	11.5	8.3	12.0	7.1	8.3	12.0	8.2	8.4	11.3	9.7	9.6	10.5	8.8	10.1	8.6	8.1	9.3
9.6	13.0	8.2	10.8	9.6	10.5	11.0	8.9	9.0	12.0	8.6	11.1	8.7	8.8	6.8	10.3	11.6	7.9	6.3	11.6
14.3	14.6	7.8	9.9	10.8	12.8	8.9	5.9	11.5	9.5	9.0	9.0	12.5	7.6	6.4	9.1	6.4	7.9	11.1	11.7
10.7	8.5	9.7	11.2	16.3	11.4	16.1	9.6	6.7	8.8	6.0	11.1	8.9	9.6	7.9	11.3	10.2	7.3	7.1	8.8
9.3	9.1	9.3	6.4	11.5	13.3	7.5	8.9	8.8	8.8	8.7	8.6	9.2	7.4	7.1	11.9	8.6	8.3	11.0	8.3
9.9	11.1	8.5	10.3	9.6	9.4	10.2	7.4	7.7	7.7	10.0	9.5	7.4	9.6	7.9	8.3	9.2	7.8	8.0	8.6
8.9	7.5	11.1	11.5			10.4	9.2	7.8	8.3	8.0	7.2	9.6	9.8	7.4	8.9	8.6	5.7	10.5	8.5
9.4	6.5	8.7	9.2			7.3	9.4	8.2	6.6	7.4	8.0	9.8	8.3	7.8	6.6	8.0	10.3	9.4	8.9
7.4	7.1	5.3	8.7			7.4	8.4	9.2	7.3	8.6	9.4	8.6	9.8	8.5	7.9	8.8	9.3	6.3	8.9
6.9	7.8	7.3	6.8			8.0	5.3	6.7	8.3	9.4	7.0	8.5	14.0	7.4	8.6	7.6	8.6	8.3	7.9
8.7	6.8	7.1	8.8			5.1	7.3	7.9	9.5	6.3	7.6	5.5	7.8	7.4	6.6	4.9	9.5	10.9	8.2
6.8	7.2	6.5	6.8			7.9	8.8	6.6	5.6	7.8	9.4	8.1	8.8	6.8	8.0	8.8	8.5	8.1	8.2
8.9	7.0	7.7	5.8			6.3	8.5	6.2	6.5	9.4	9.3	7.8	5.9	8.1	7.8	8.8	8.0	7.4	8.6
7.1	9.2	6.8	6.8			6.3	7.9	6.8	8.3	6.5	9.7	8.0	5.1	7.5	7.0	8.5	7.3	8.0	7.1
7.8	8.0	9.9	9.4			6.2	8.2	6.0	6.6	8.6	7.1	9.8	5.5	7.1	6.4	6.5	9.1	8.6	9.6
6.4	9.1	8.1	7.5			5.7	7.6	5.7	5.5	5.3	6.7	8.5	6.4			7.0	7.9	9.1	7.8
6.5	7.0	6.0	9.7			6.3	5.2	6.0	6.3	6.0	7.5					6.2	5.7	8.0	6.1
								6.3	6.1	7.3	6.8							7.2	6.0
								6.7	6.3	7.3	5.5							8.0	8.7
								6.7	6.8	5.8	5.5							6.7	6.0

TABLE 1 (continued)

Coefficients of Variation.

D/3b		E/1a		E/1b		E/2a		E/2b		E/3a		E/3b		F/1		F/2		F/3	
♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
7.3	10.1	9.2	9.9	8.9	10.2	11.7	10.6	9.3	10.2	8.3	7.4	9.8	8.7	10.2	13.3	9.7	11.6	10.9	8.7
7.5	7.8	12.4	11.0	9.8	11.6	9.3	9.1	9.5	9.5	11.7	8.2	10.6	11.0	12.0	12.9	8.7	10.4	8.8	12.7
10.3	11.8	10.5	12.4	13.2	9.7	7.0	9.1	6.3	9.0	9.2	8.7	9.6	9.9	8.6	9.6	8.1	8.0	12.6	10.6
10.6	9.9	12.2	9.0	12.1	11.4	7.6	6.4	8.1	8.3	11.6	10.0	10.8	10.7	8.5	10.8	7.2	8.9	8.2	10.0
9.1	13.6	10.4	10.5	7.5	10.9	5.7	9.6	9.7	8.4	11.4	11.8	6.9	11.6	9.1	10.3	6.6	8.2	8.0	8.7
8.5	9.5	8.3	6.9	9.9	9.6	7.8	8.2	8.4	9.4	10.6	11.7	9.1	13.1	7.5	9.4	7.9	7.2	8.5	8.1
9.0	9.0	9.2	8.3	11.3	9.9	8.3	7.3	7.0	10.2	10.8	8.7	10.6	7.0	7.5	10.5	7.9	7.8	7.7	9.3
7.5	8.2	6.9	8.8	9.9	10.1	7.3	9.4	8.0	8.5	8.3	10.2	8.7	7.3	9.2	11.6	6.4	7.9	7.0	8.7
9.4	6.6	7.9	7.8	7.6	7.7	7.1	9.1	8.4	9.8	7.3	7.3	11.1	9.6	8.4	9.3	6.5	6.2	7.8	8.7
9.0	8.8	7.8	9.8	8.1	8.4	6.0	8.1	9.9	10.1	6.9	6.7	7.3	9.6	8.1	8.5	6.4	8.4	9.8	8.5
8.5	9.4	11.0	9.3	6.2	8.1	7.7	9.3	10.7	10.4	8.3	9.9	9.0	8.3	10.6	9.3	8.2	9.2	6.2	8.9
7.5	8.3	8.4	8.4	7.5	8.4	7.0	7.0	8.3	8.9	9.1	9.6	7.9	8.8	9.9	7.4	8.0	8.3	6.6	7.7
9.7	8.2	9.7	9.1	7.3	6.1	8.1	7.0	10.4	9.6	6.7	9.3	8.9	7.8	11.8	8.4	8.8	9.2	9.5	7.3
8.5	7.4	8.9	9.8	7.5	8.8	9.3	8.8	8.6	8.0	8.2	5.8	8.4	9.5	7.4	9.9	7.1	9.3	4.8	9.1
8.1	8.9	6.7	9.3	7.3	6.3	6.8	8.7	8.5	8.2	8.2	8.1	9.1	7.9	10.3	9.5	6.8	10.9	6.2	8.4
9.0	5.5	7.9	7.5	9.3	6.2	9.4	7.7	9.7	9.2	6.2	8.6	9.1	5.8	9.4	11.8	7.1	10.5	6.2	9.0
8.5	7.3					7.4	6.5	8.1	10.7	9.3	8.0	9.0	11.3	9.1	10.0	7.9	7.6	6.9	9.0
6.9	5.9					7.2	6.3	7.2	7.6	7.1	6.4	6.6	7.2	8.7	8.3	7.8	5.9	6.6	8.3
5.6												9.3	8.7	8.6	9.7	7.9	7.1	8.2	9.0
8.6	7.8											8.6	6.7	8.4	7.1	7.4	8.4	7.8	8.2
7.4	8.1											7.0	6.5	10.8	8.0	9.4	10.8	10.2	9.7
7.2	6.9													7.8	10.8	5.8	8.4	9.9	10.1
5.7	6.3													8.8	10.8	8.9	9.5	6.1	8.0
														7.9	12.1	11.2	7.0	6.7	8.7
														8.3	7.9	7.9	9.5	7.0	9.8
														8.8	8.2	7.0	8.0	6.4	8.1

TABLE 1 (continued)

Coefficients of Variation.

H/1		H/2		H/3		H/4		H/5		G/1		G/2		G/3		G/4		G/5	
♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
7.5	13.2	9.5	10.6	10.0	8.2	10.8	11.0	9.1	10.6	11.3	6.4	12.0	9.9	8.0	8.5	5.8	10.4	8.3	7.6
10.3	7.7	8.8	11.4	9.5	10.2	10.4	8.5	7.1	11.7	12.2	8.7	8.1	8.1	9.4	6.9	7.3	10.1	8.2	11.6
10.0	10.7	5.9	8.8	7.2	7.3	10.3	10.3	10.7	11.7	8.5	8.9	8.4	8.0	5.9	6.9	7.5	9.3	7.4	8.9
6.2	8.8	10.0	10.4	10.5	10.3	9.0	9.4	8.3	10.2	7.4	8.7	7.6	7.1	6.4	8.9	7.9	10.4	10.7	8.8
8.4	8.1	8.1	8.4	8.1	7.8	5.8	8.1	6.3	8.3	6.4	9.7	5.7	9.3	8.3	9.4	10.9	10.4	7.9	8.4
10.6	8.3	7.4	7.6	8.6	10.8	7.7	8.1	8.0	9.2	8.4	8.0	7.4	9.8	9.3	10.5	9.7	11.0	6.7	7.4
6.3	8.5	10.3	8.1	7.5	6.9	8.5	7.4	7.0	9.3	7.8	8.6	7.8	9.1	7.3	9.8	8.0	11.7	5.0	8.5
7.9	9.1	5.9	8.8	7.7	7.6	6.5	6.2	7.6	9.0	6.6	9.0	7.4	6.6	7.3	7.4	9.5	8.7	6.4	8.1
6.0	6.8	8.0	7.2	6.9	12.5	7.5	8.1	9.3	11.6	6.1	6.9	5.2	7.4	9.6	9.5	10.0	9.8	8.2	7.5
5.6	8.6	7.2	9.1	6.9	7.8	7.2	8.7	6.3	8.5	9.7	10.7	5.7	7.4	8.0	10.4	8.8	10.2	7.4	7.2
6.5	7.6	6.3	7.1	7.5	7.0	8.0	10.9	6.7	9.6	8.2	5.9	6.5	9.1	8.2	10.6	11.4	10.5	10.0	7.3
8.7	9.9	6.1	5.7	7.7	6.1	8.8	5.8	8.7	8.5	7.7	10.1	5.5	6.2	5.7	7.8	8.7	9.9	7.1	7.6
7.8	9.4	8.0	8.3	7.9	6.6	6.6	9.4	7.3	7.7	8.0	10.7	8.2	7.4	6.7	8.4	9.6	8.8	7.8	9.2
8.3	9.3	7.7	6.1	6.4	7.8	7.6	9.1	7.3	7.5	6.4	9.0	6.9	7.5	9.4	11.1	8.1	10.8	5.8	7.2
6.5	9.3	7.9	8.2	5.9	7.6	6.4	7.8	8.5	8.7	7.0	9.1	6.6	7.3	7.2	10.0	6.4	7.5	6.3	8.7
5.6	9.3	8.3	8.2	7.4	9.1	7.7	7.3	6.3	8.5	7.8	8.7	7.6	8.3	6.0	6.5	9.6	7.4	6.8	8.2
6.2	9.1	7.5	8.0	6.4	7.0	7.2	9.9	6.7	6.8	6.0	8.3			6.9	10.0				
6.9	6.2	8.8	7.0	9.1	6.9	5.8	8.1	7.4	6.7										

TABLE 2

Lines	Generations 0	5	10	15	20	25	Lines	Generations 0	5	10	15	20	25
C/1	0.98	0.98	1.05	1.04	1.09	-	E/1a	1.08	1.04	1.04	1.04	-	-
C/2	1.06	1.01	1.07	1.05	1.06	-	E/1b	1.06	1.02	1.07	1.10	-	-
C/3	1.07	1.01	1.07	1.07	1.07	1.10	E/2a	1.03	.96	.99	1.04	-	-
B/1	1.06	.97	1.09	1.02	-	-	E/2b	1.03	.96	1.01	.92	-	-
B/2	1.05	1.03	1.11	1.10	1.10	-	E/3a	1.04	1.04	1.03	1.08	-	-
B/3	.99	1.02	1.01	1.02	-	-	E/3b	1.01	1.03	1.04	1.04	-	-
B/4	.99	1.01	1.05	1.03	-	-	F/1	1.06	1.05	.99	.99	1.02	1.01
B/5	1.03	1.02	1.00	1.05	-	-	F/2	1.02	1.07	1.08	1.02	1.01	.98
A/1	.98	1.03	1.06	1.03	-	-	F/3	1.00	1.06	1.07	1.05	.94	1.07
A/2	1.01	1.02	1.07	1.03	-	-	H/1	.97	1.04	1.07	1.05	-	-
A/3	1.03	1.02	-	-	-	-	H/2	1.02	1.04	.99	1.04	-	-
A/4	1.05	1.06	1.09	1.03	-	-	H/3	1.03	1.05	1.13	1.12	-	-
A/5	.99	1.04	1.03	1.06	1.05	-	H/4	1.02	.98	1.00	.99	-	-
D/1a	1.06	1.02	1.05	1.07	1.05	-	H/5	.98	1.05	1.06	1.06	-	-
D/1b	1.04	1.09	1.07	1.08	-	-	G/1	1.03	.98	1.04	1.02	-	-
D/2a	1.01	1.03	.98	1.02	-	-	G/2	1.03	1.00	.99	1.02	-	-
D/2b	1.01	1.01	.99	.98	-	-	G/3	1.03	1.07	1.09	1.10	-	-
D/3a	1.03	1.05	1.02	1.01	1.03	-	G/4	1.02	1.04	1.11	1.03	-	-
D/3b	1.02	.99	1.02	.96	.99	-	G/5	.99	.99	1.07	1.08	-	-

Sex-ratio (female to male score) for all the mass-mated lines.

TABLE 3

Lines	Overall	Generations 0-5	5-10	10-15	15-20	20-25	Lines	Overall	Generations 0-5	5-10	10-15	15-20	20-25
C/1	26.93%	46.7	38.2	7.2	15.5	-	E/1a	10.74	41.4	1.2	1.1	-	-
C/2	28.31	49.6	27.4	33.0	5.0	-	E/1b	17.84	45.5	7.2	-1.1	-	-
C/3	38.30	68.2	32.2	55.3	39.5	1.8	E/2a	12.53	12.5	14.7	9.5	-	-
B/1	21.49	45.8	20.8	14.4	-	-	E/2b	15.83	14.6	30.9	5.3	-	-
B/2	27.30	51.79	17.4	46.3	-6.8	-	E/3a	20.06	22.8	21.4	12.4	-	-
B/3	6.71	39.4	5.8	3.6	-	-	E/3b	22.52	45.1	26.9	11.9	8.8	-
B/4	13.13	28.7	14.9	10.0	-	-	F/1	25.13	40.4	50.0	47.2	14.5	-0.10
B/5	10.6	28.10	-3.2	27.4	-	-	F/2	18.03	30.6	25.9	13.5	19.0	1.66
A/1	19.60	19.1	31.1	6.9	-	-	F/3	19.18	37.6	41.7	12.6	24.8	-0.20
A/2	9.42	23.6	8.0	19.0	-	-	H/1	17.39	36.8	23.4	-0.6	-	-
A/3	11.43	15.9	-	-	-	-	H/2	22.34	41.5	14.4	13.1	-	-
A/4	18.88	25.3	32.7	3.8	-	-	H/3	14.00	16.4	26.3	0.8	-	-
A/5	26.58	47.4	33.3	14.6	32.8	-	H/4	11.89	10.3	18.6	3.5	-	-
D/1a	23.55	32.1	35.7	23.5	23.1	-	H/5	26.64	49.9	22.5	11.3	-	-
D/1b	15.61	41.0	19.1	6.8	-	-	G/1	14.12	26.8	9.3	10.6	-	-
D/2a	18.26	46.0	24.5	10.4	-	-	G/2	9.77	12.9	5.8	9.9	-	-
D/2b	18.08	64.0	8.9	19.0	-	-	G/3	22.80	21.9	7.7	16.0	-	-
D/3a	19.59	49.7	21.3	21.0	10.5	-	G/4	13.58	24.7	6.6	8.4	-	-
D/3b	23.57	50.0	31.6	14.1	24.0	-	G/5	13.78	20.51	5.4	13.4	-	-

Realized heritabilities for all the mass-mated lines.

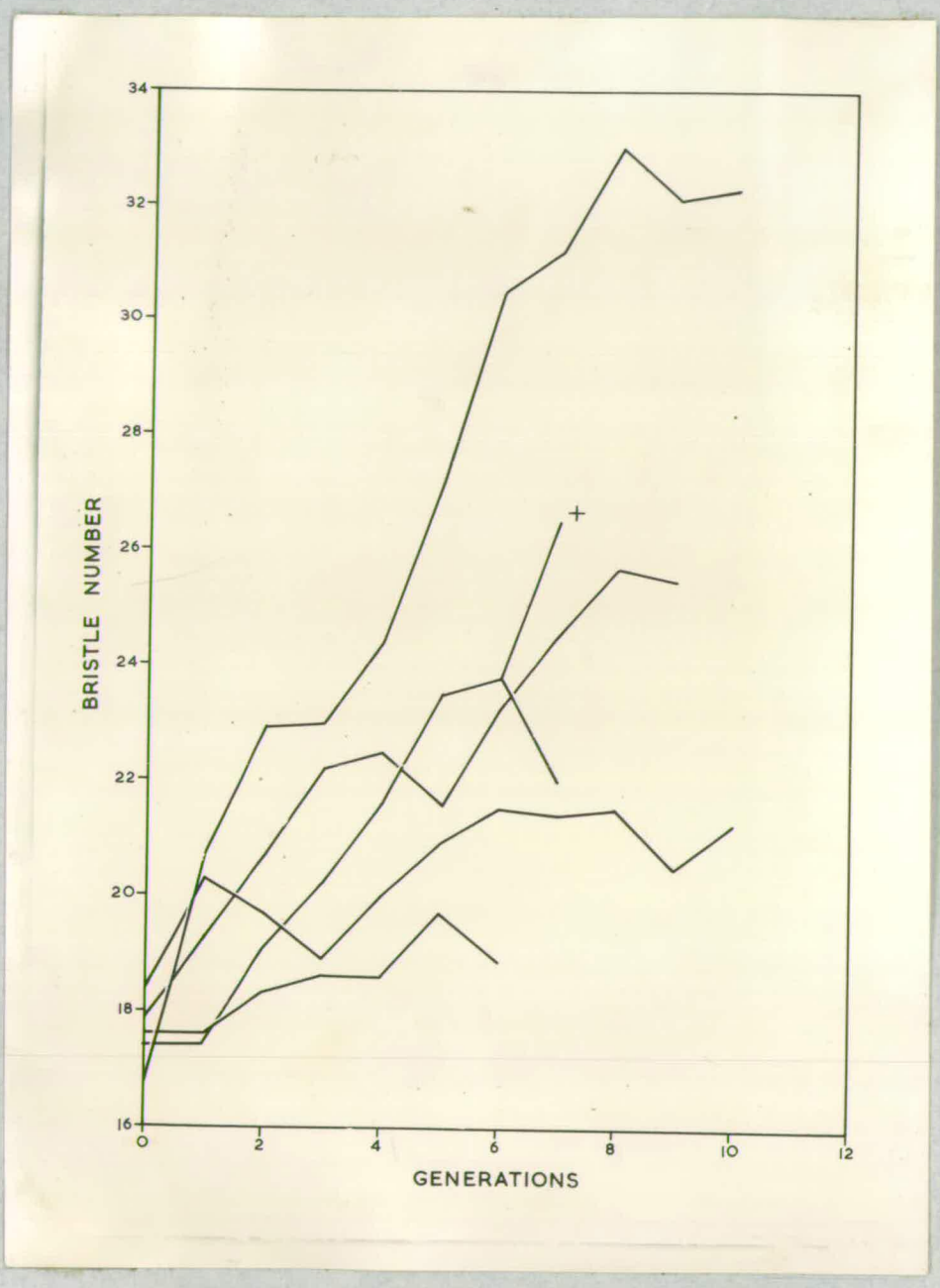

FIGURE 1. Response to selection. Selection intensity 1 out of 5 of each sex. Generation means based on average of male and female scores.

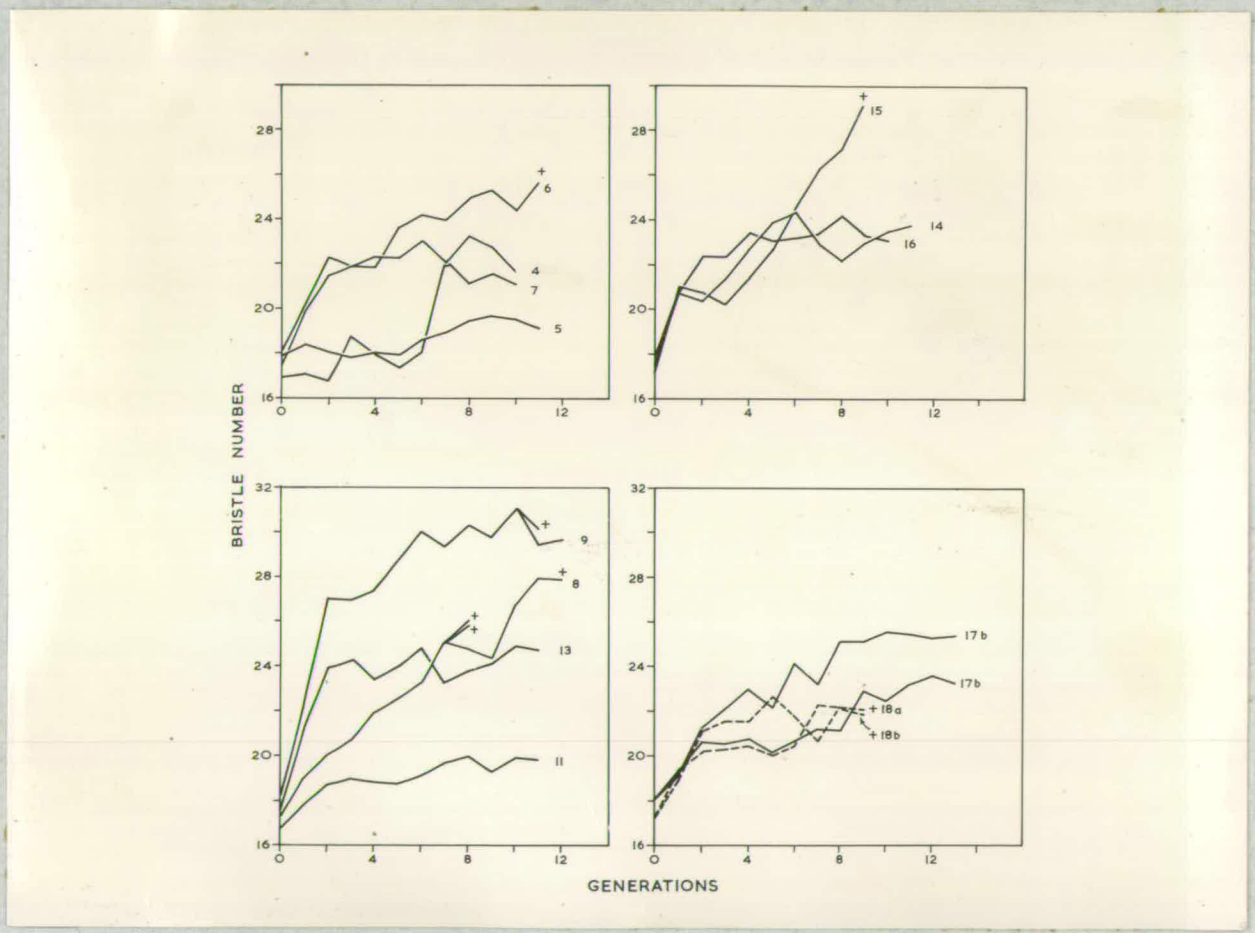

FIGURE 2. Response to selection. Selection intensity 1 out of 5 of each sex. Generation means based on average of male and female scores.

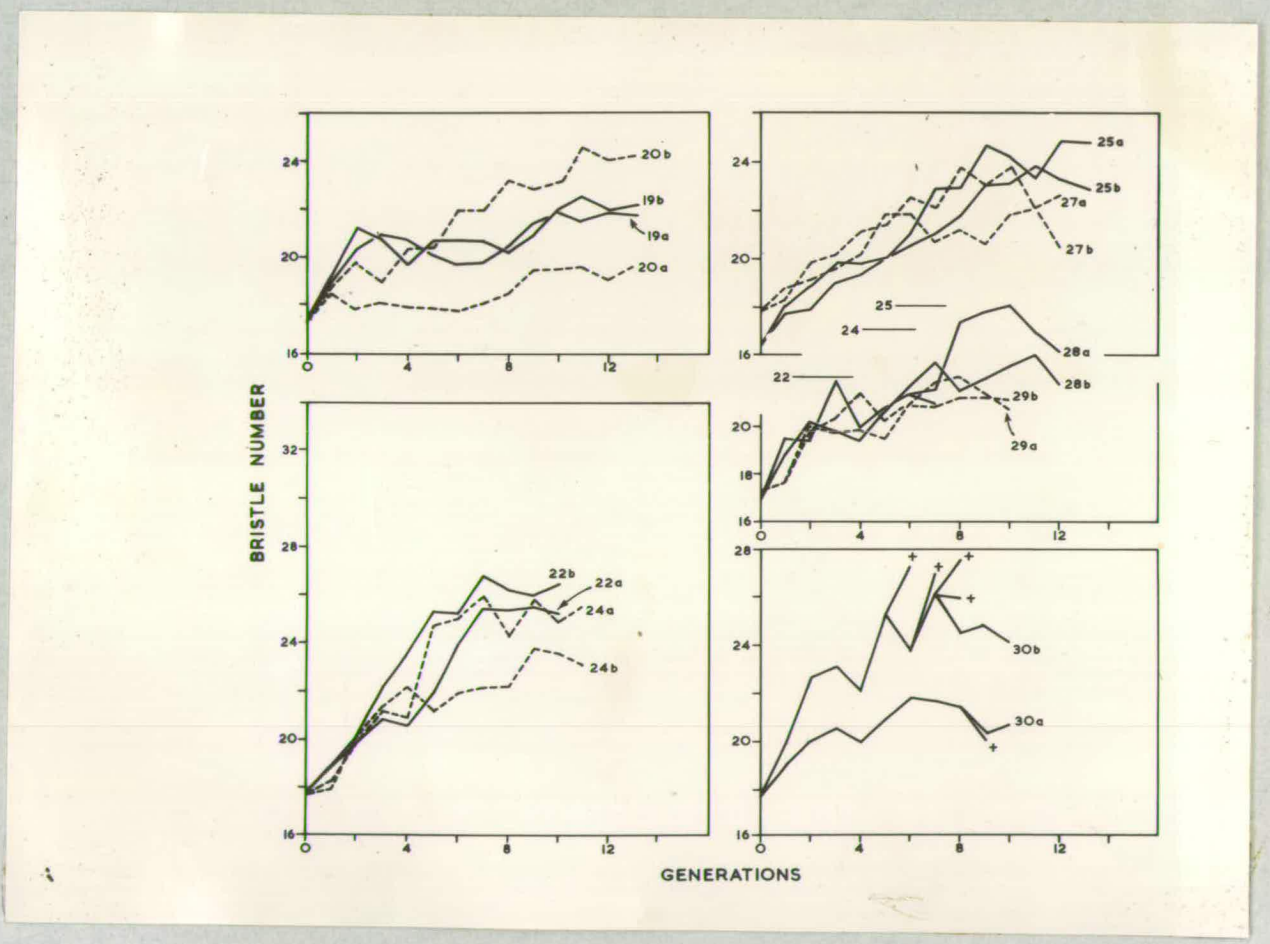

FIGURE 3. Response to selection. Selection intensity 1 out of 5 of each sex. Generation means based on average of male and female scores.

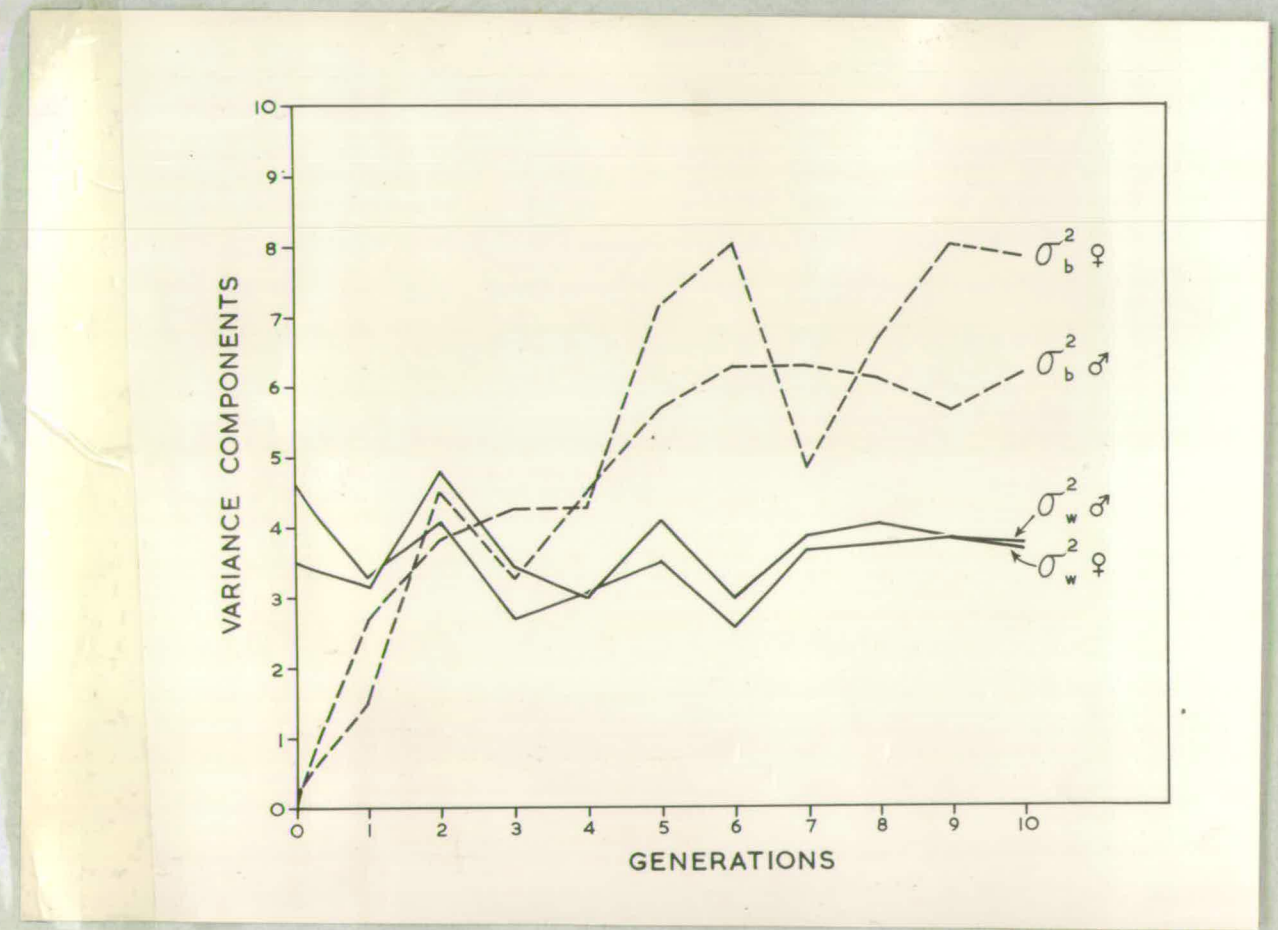

FIGURE 4. Within and between line variance components for each generation for the two sexes.

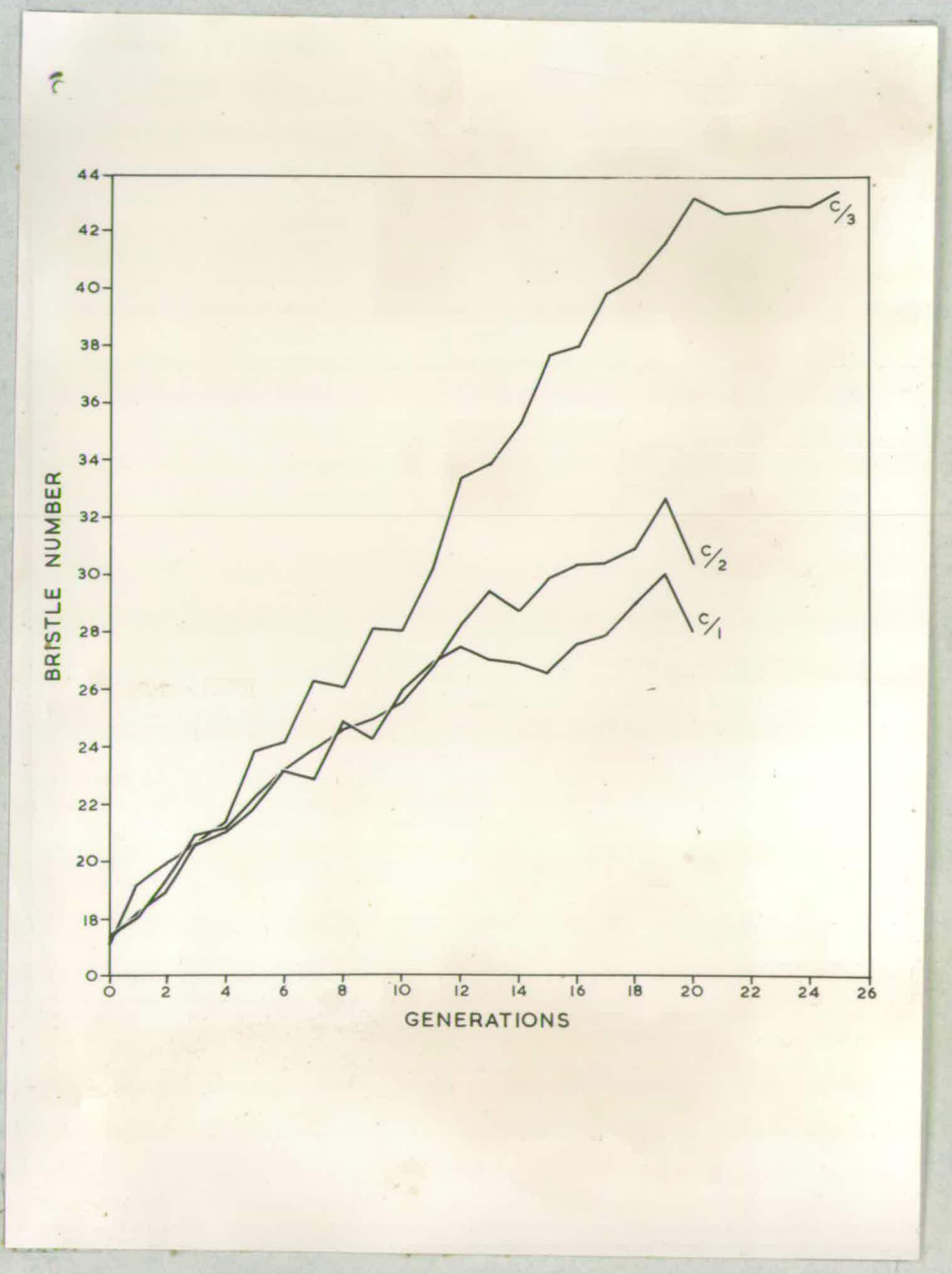

FIGURE 5. Response to selection. Mass-mated lines started from the base population. Selection intensity 10 out of 25 of each sex. Generation means based on average of male and female scores.

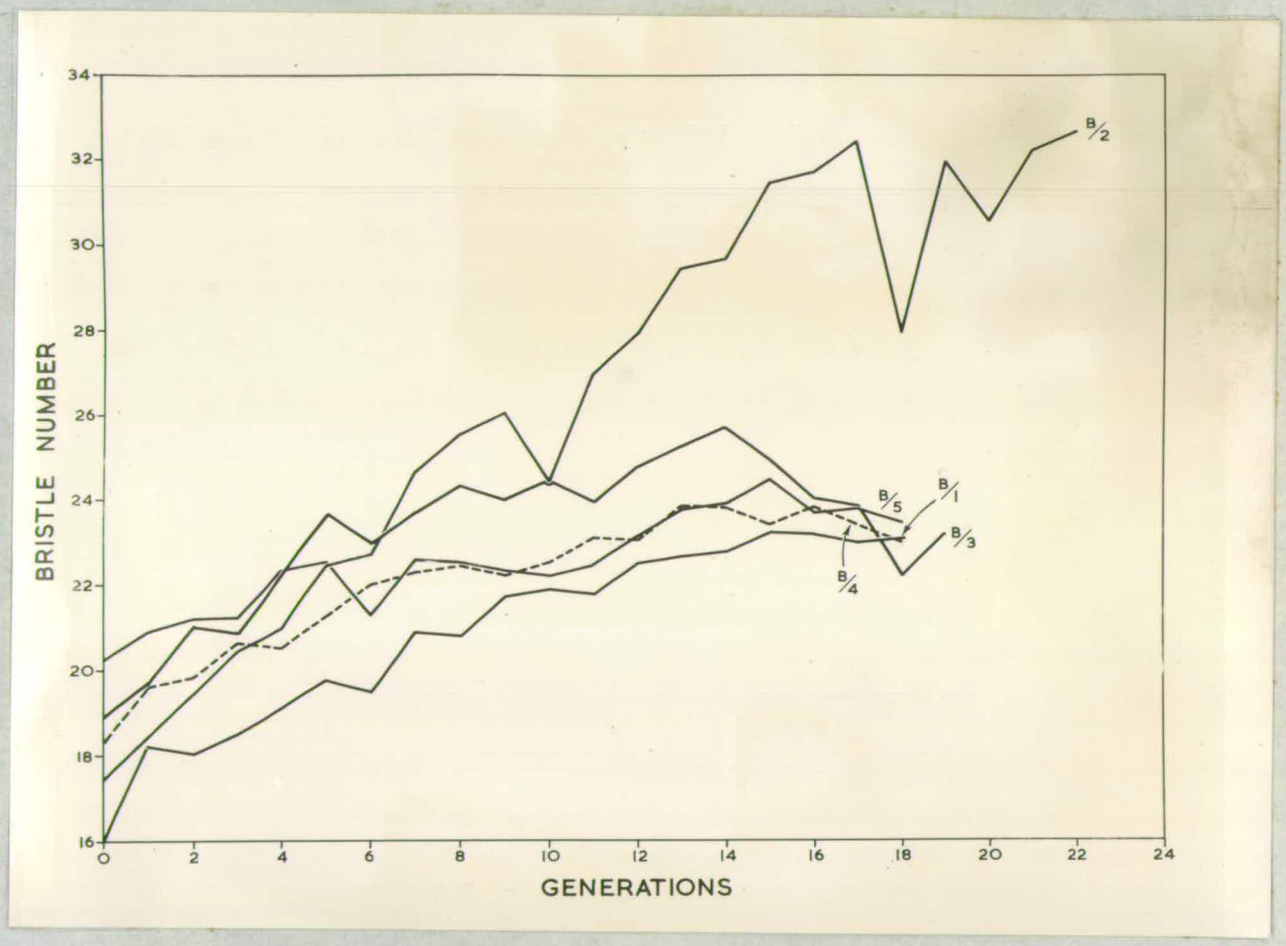

FIGURE 6. Response to selection. Mass-mated lines started after one restrictive mating. Selection intensity 10 out of 25 of each sex. Generation means based on average of male and female scores.

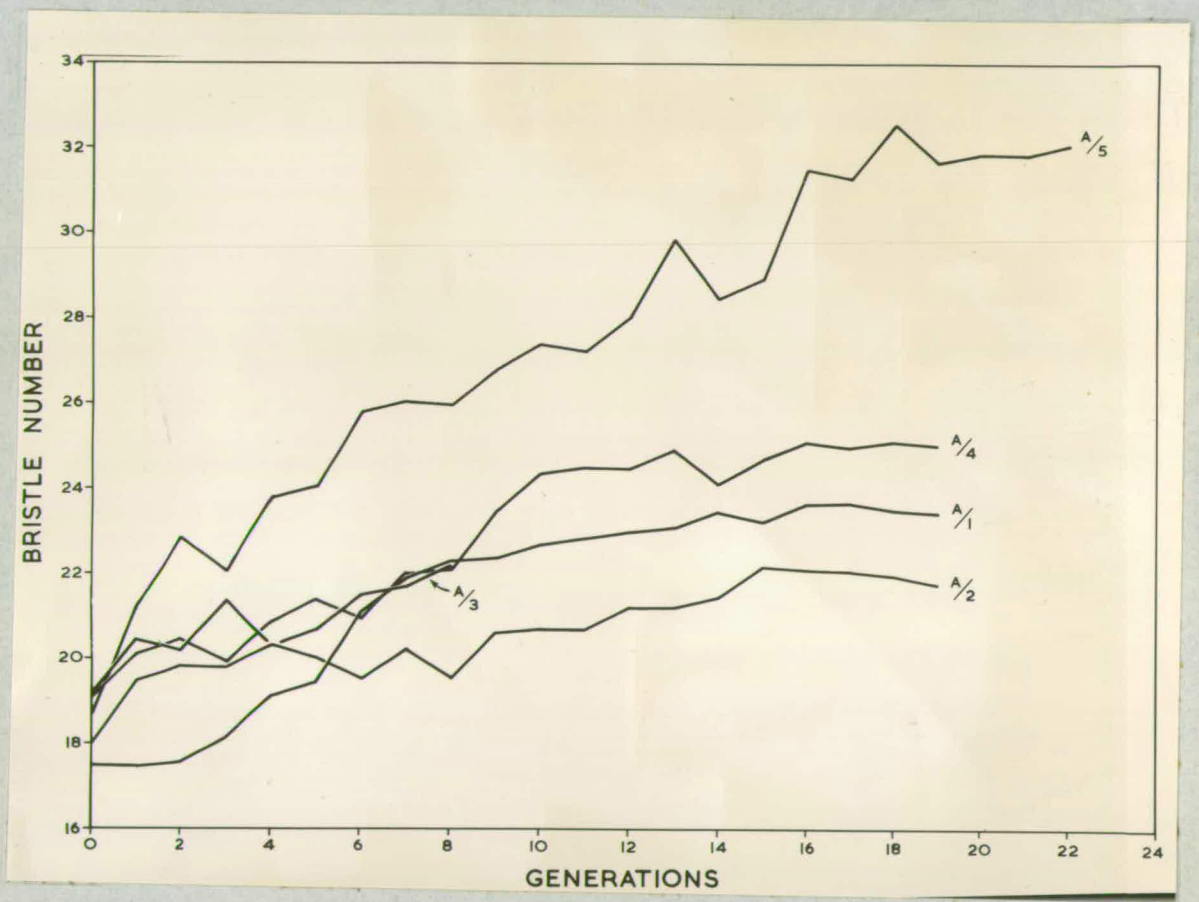

FIGURE 7. Response to selection. Mass-mated lines started after 3 restrictive matings. Selection intensity 10 out of 25 of each sex. Generation means based on average of male and female scores.

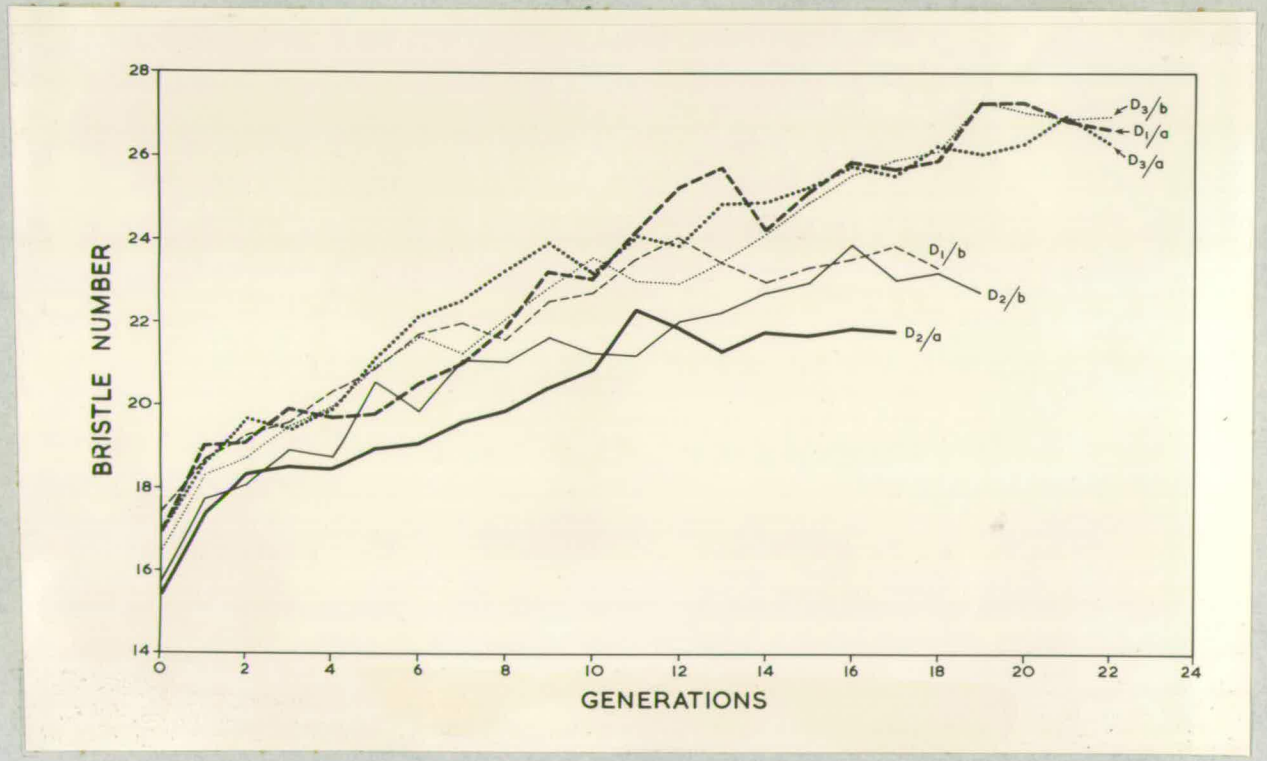

FIGURE 8. Response to selection. Mass-mated lines started after 1 restrictive mating. Selection intensity 10 out of 25 of each sex. Generation means based on average of male and female scores. The pairs of lines are indicated by the use of a continuous line, broken lines and dotted lines.

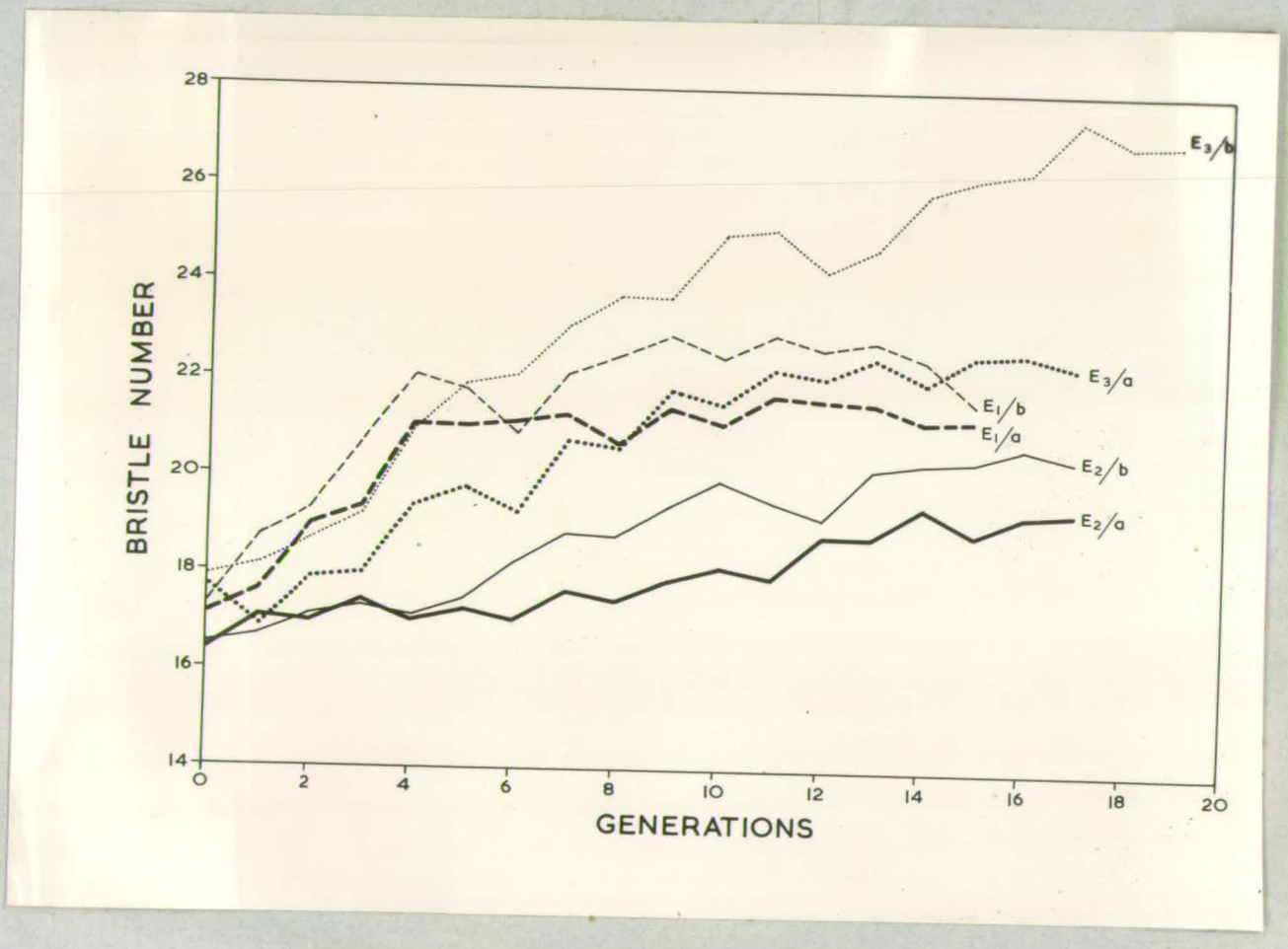

FIGURE 9. Response to selection. Mass-mated lines started after 3 restrictive matings. Selection intensity 10 out of 25 of each sex. Generation means based on average of male and female scores. The pairs of lines are indicated by the use of continuous lines, broken lines and dotted lines.

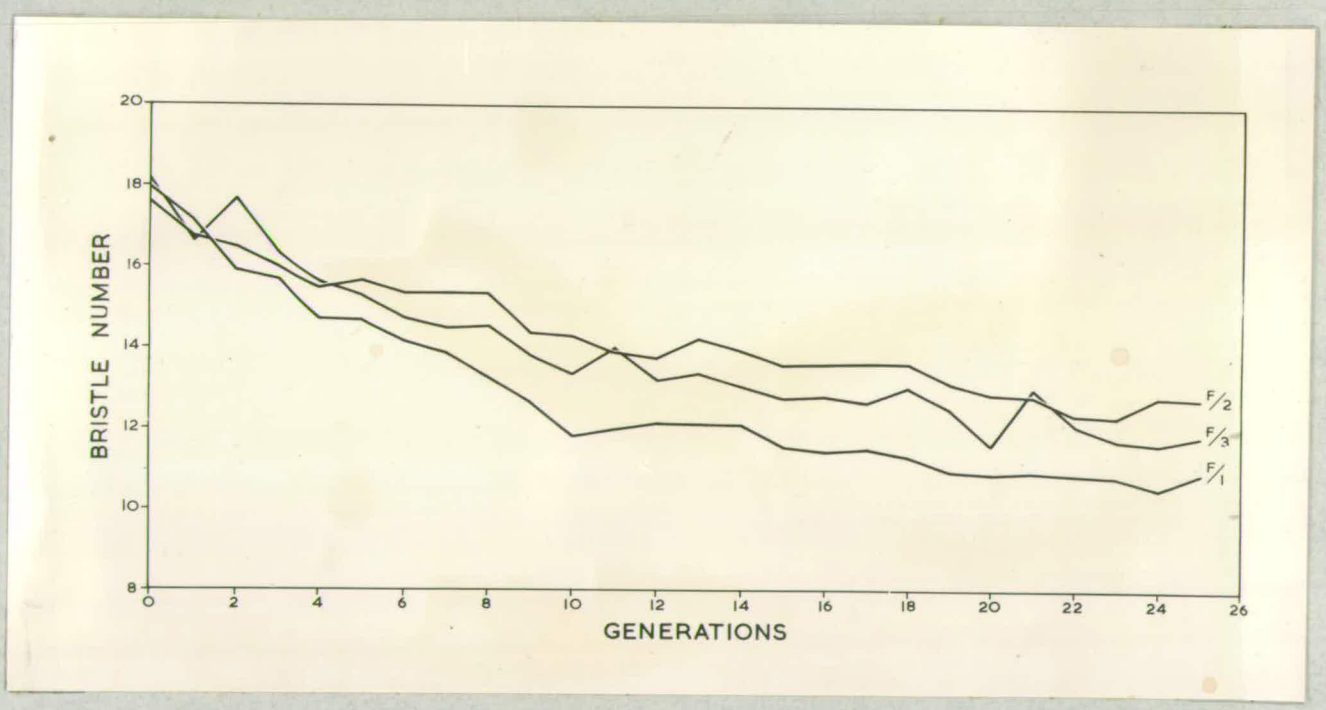

FIGURE 10. Response to selection. Mass-mated lines started from the base population. Selection intensity 10 out of 25 of each sex. Generation means based on average of male and female scores.

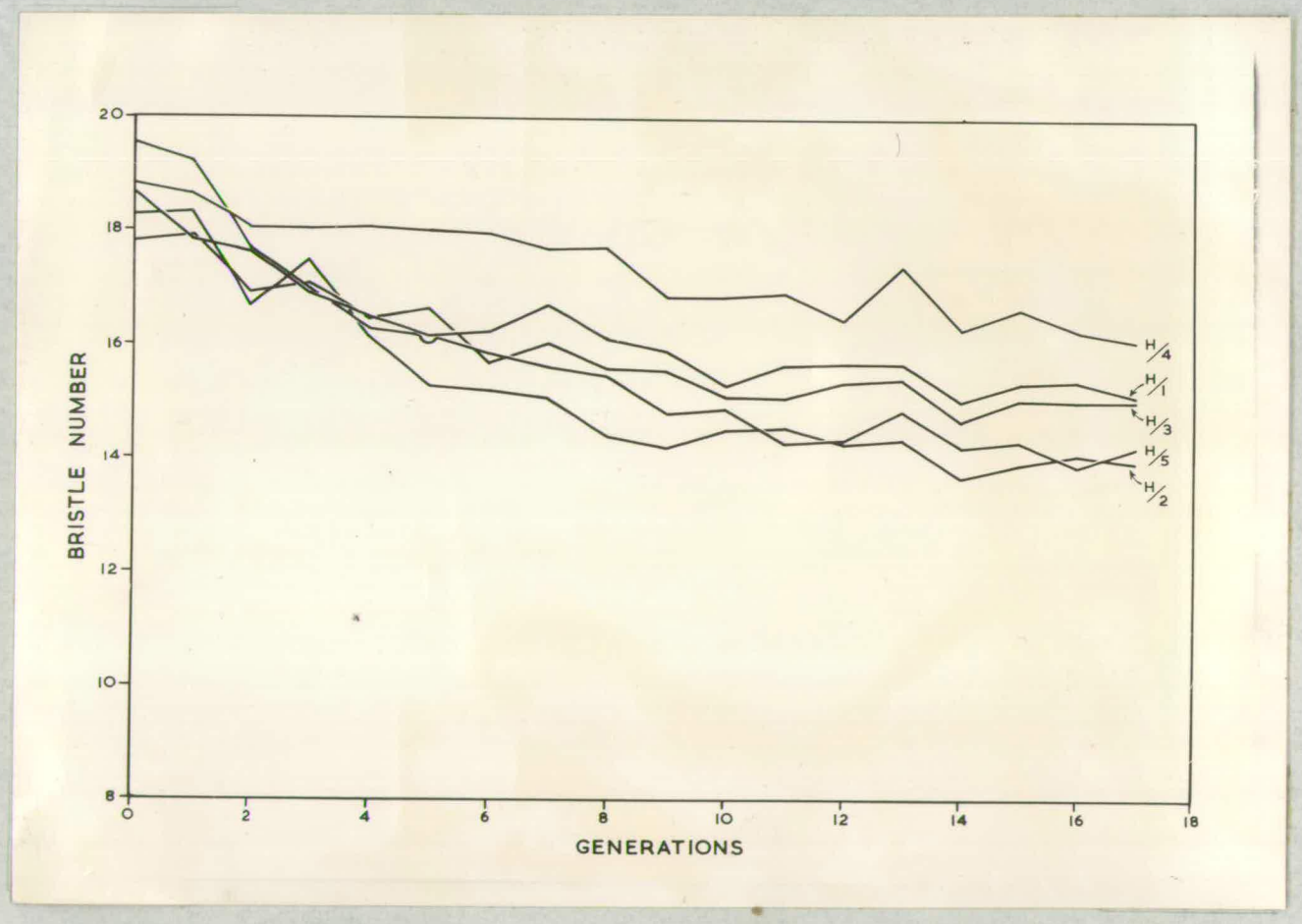

FIGURE 11. Response to selection. Mass-mated lines started after one restrictive mating. Selection intensity 10 out of 25 of each sex. Generation means based on average of male and female scores.

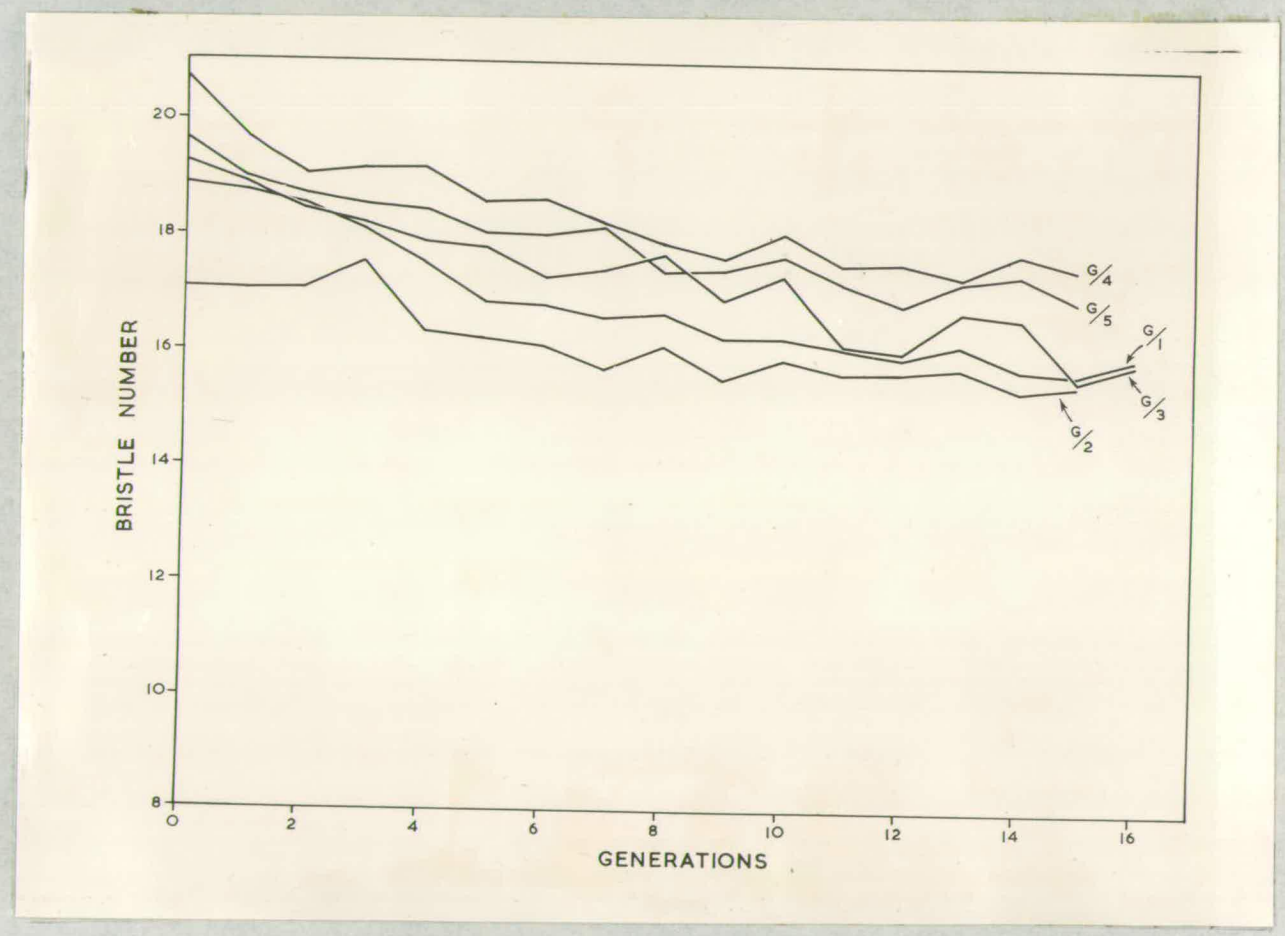

FIGURE 12. Response to selection. Mass-mated lines started after 3 restrictive matings. Selection intensity 10 out of 25 of each sex. Generation means based on average of male and female scores.

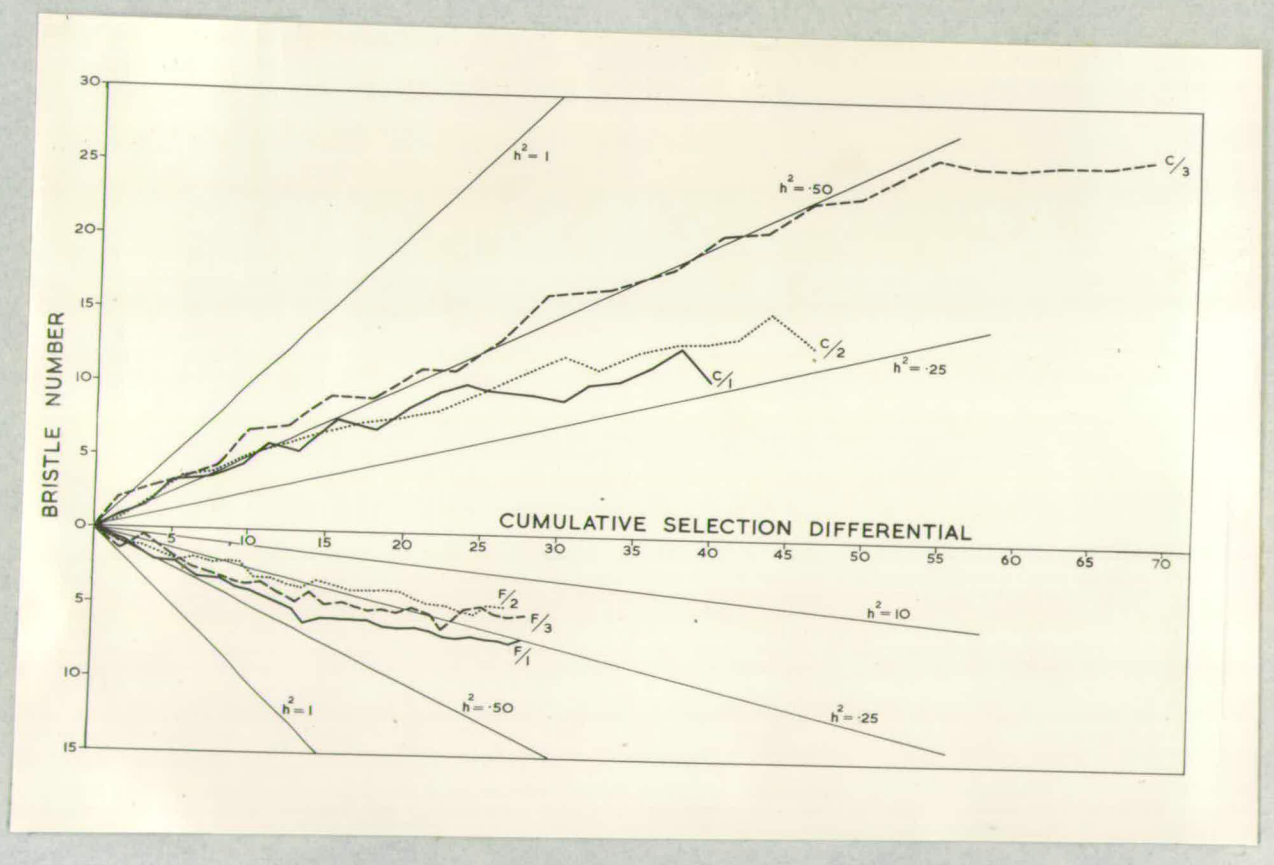

FIGURE 13. The relationship between response to individual selection (as in Figures 6 and 10) and the cumulative selection differential. The slope of the line at any generation is an indication of the realised heritability. Unrestricted mass-mated lines.

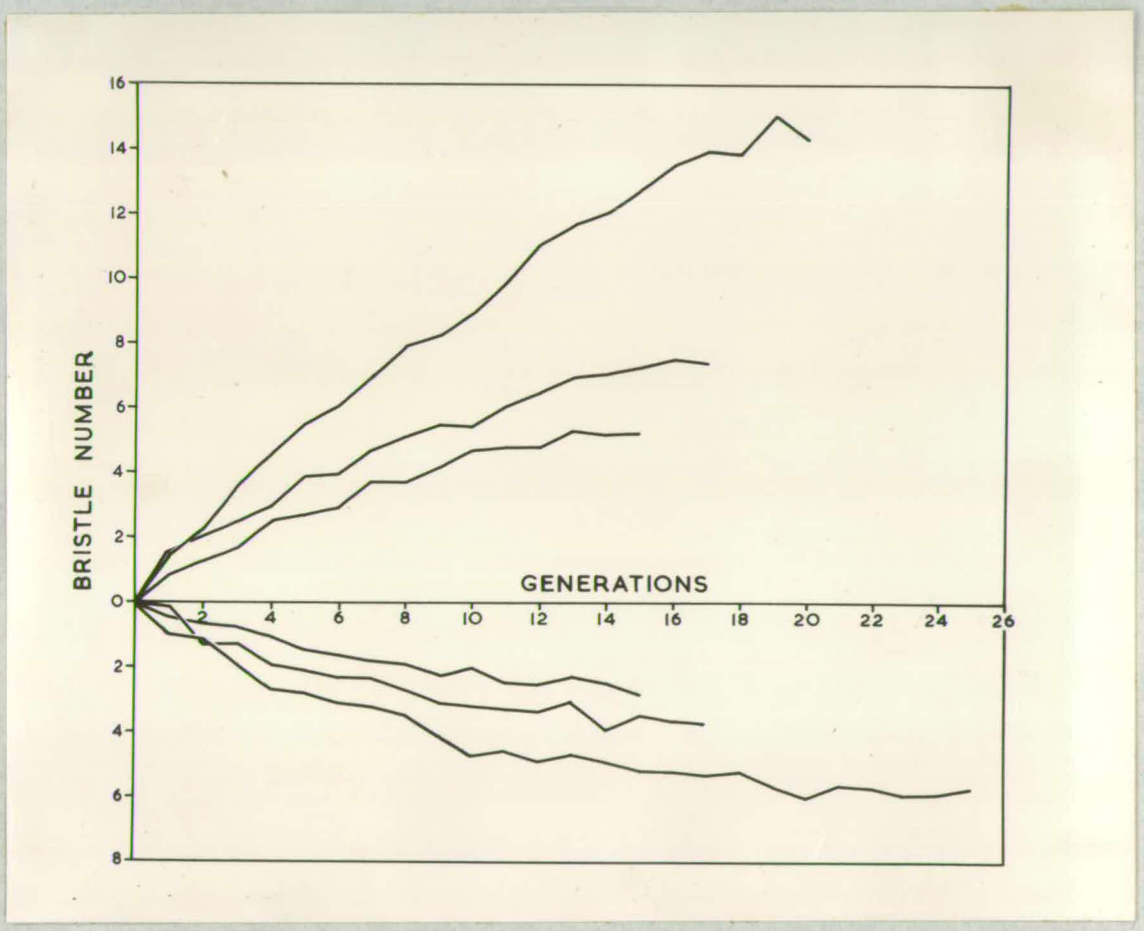

FIGURE 14. Mass-mated lines represented in Figures 6 and 10. Rate of response to selection. A common origin given to all lines. Arithmetic scale.

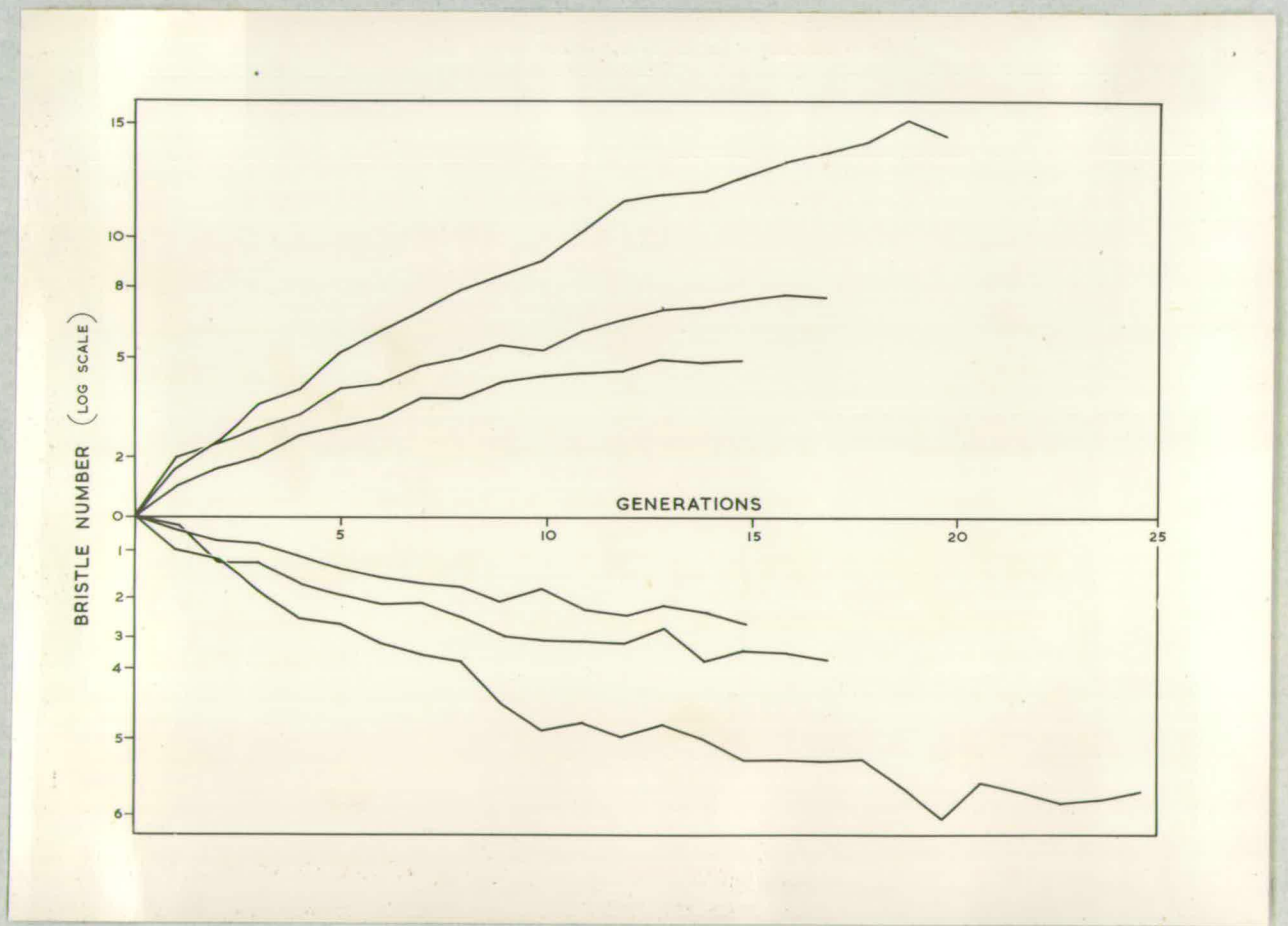

FIGURE 15. Mass-mated lines represented in Figures 5 and 10. Rate of response to selection. A common origin given to all lines. A logarithmic scale.

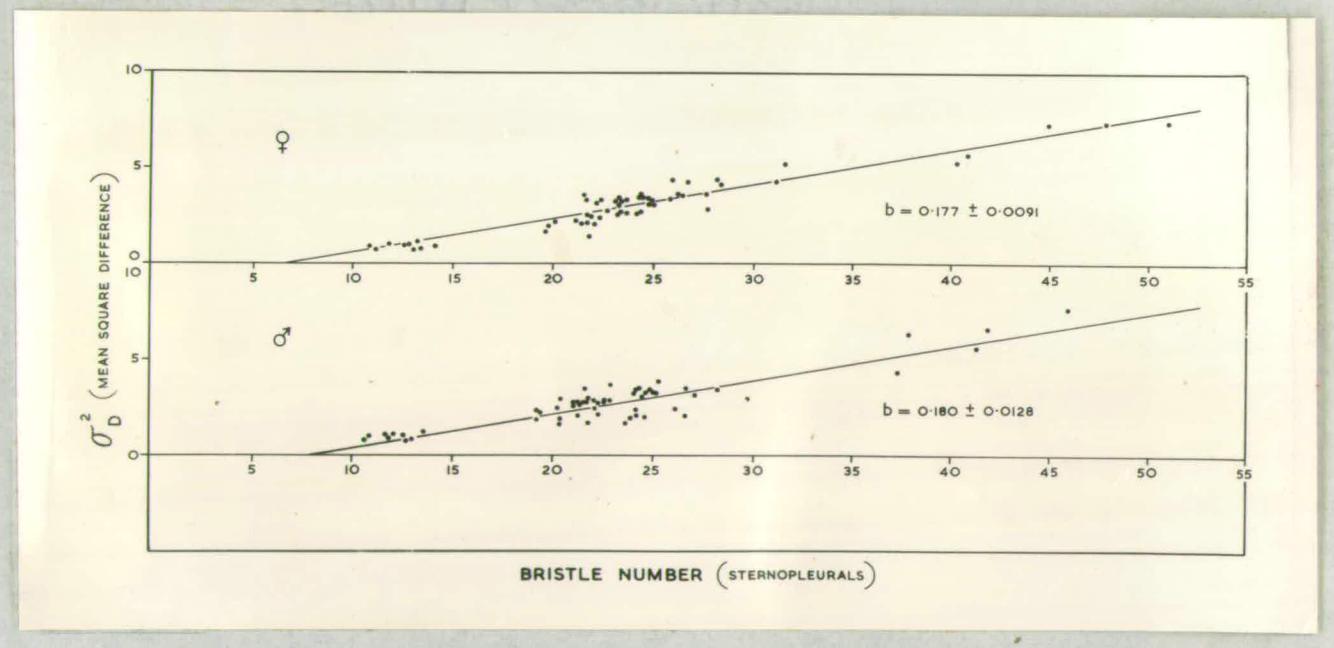

FIGURE 16. Regression of mean square difference between left and right sides on total count of sternopleurals. Points of full-sib lines mass-mated lines based on 60 and 100 flies (respectively).

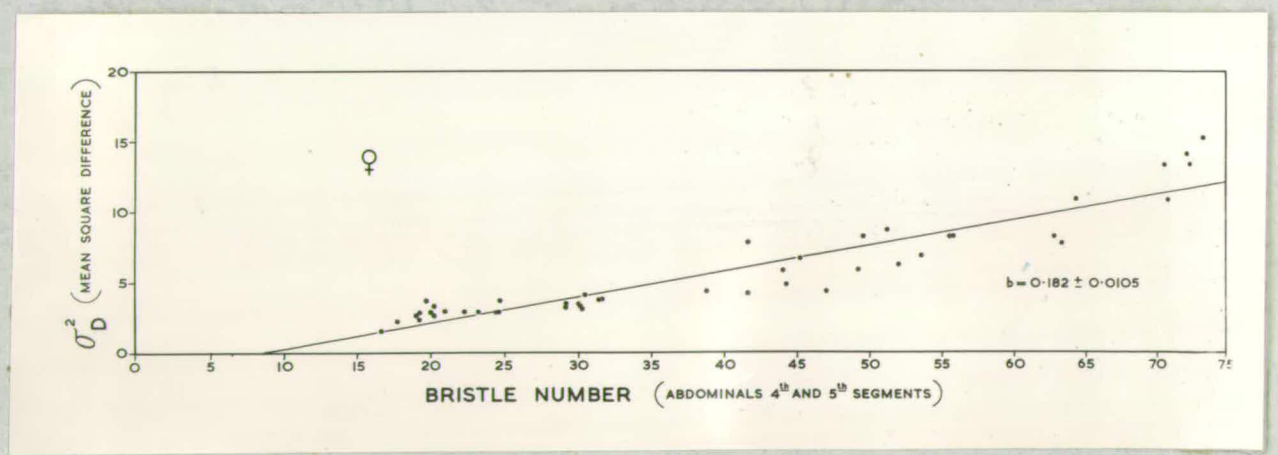

FIGURE 17. Regression of mean square difference between sternital counts of the 4th and 5th abdominal segments on total of those two segments. Each point based in 100 flies.

REFERENCES.

BELL, A.C., MOORE, C.H. and WARREN, D.C. 1955. The evaluation of new methods for the improvement of quantitative characters. Cold Spr. Harb. Symp. Quant. Biol., 20: 197-211.

BRIDGES, C.B. and BREHME, K.S. 1944. The Mutants of Drosophila melanogaster. Washington, D.C. Carnegie Institution of Washington. Publication 552. Second Printing vii + 257.

BRILES, W.E., McGIBBON, W.H. and IRWIN, M.R. 1950. On multiple alleles affecting cellular antigens in the chicken. Genetics 35: 633-652.

BRILES, W.E. 1954. Evidence for overdominance of the B blood group alleles in the chicken. Genetics, 39: 961-962.

BRILES, W.E., ALLEN, C.P. and MILLEN, T.W. 1957. The B blood group system of chickens. I. Heterozygosity in closed populations. Genetics, 42: 631-648.

CLARKE, J.M., MAYNARD SMITH, J. and SONDHI, K.C. 1961 Asymmetrical response to selection for rate of development in Drosophila subobscura. Genetical Research, 2: 70-81.

CLAYTON, G.A., MORRIS, J.A. and ROBERTSON, Alan. 1957. An experimental check on quantitative genetical theory. I. Short term response to selection. J. Genetics, 55: 131-151.

CLAYTON, G.A. and ROBERTSON, Alan. 1957. An experimental check on quantitative genetical theory. II. The long term effects of selection. J. Genetics, 55: 152-170.

COOKS, Betty. 1954. Polygenic systems controlling the expression of major mutant genes which affect chaetta number in Drosophila in Drosophila melanogaster. Heredity. 13 34.

CROW, J.F. 1954. Breeding structure of populations. II. Effective population number. Statistics in Mathematics and Biology. Ames, U.S.A. Iowa State Coll. Press.

DEMPSTER, E.R., and LERNER, I.M. 1947. The optimum structure of breeding flocks. Genetics 22: 555-579.

DEMPSTER, E.R. 1955. Genetic models in relation to animal breeding problems. Biometrics, 11: 535-536.

DICKERSON, G.E. 1951. Effectiveness of selection. A symposium presented at the 1949 meeting of the American Society of Animal Production. For economic characters in swine. Journal of Animal Science. Vol. 10, No. 1. 12-17.

DICKERSON, G.E. 1955. Genetic slipage in response to selection for multiple dijectives. Cold Spr. Harb. Symp. Quant. Biol. 20: 213-224.

FALCONER, D.S. 1953. Selection for large and small size in mice. J. Genetics, 51: 470-501.

FALCONER, D.S. 1960. Selection of mice for growth on high and low planes of nutrition. Genetical Res. 1: 91-113.

FALCONER, D.S. and LATYSZEWSKI, M. 1952. Selection for size in mice on high and low planes of nutrition. Quantitative Inheritance. London. H.M.S.O. 141-151.

FALCONER, D.S. and KING, J.W.B. 1953. A study of the inheritance of body weight in the albino mouse by selection. J. of Heredity, 29, 101-112.

LERNER, I.M. 1954. Genetic Homeostasis. Edinburgh: Oliver and Boyd. vii + 134 pp.

LERNER, I.M. and DEMPSTER, E.R. 1951. Attenuation of genetic progress under continued selection in poultry. Heredity, 5: 75-94.

LERNER, I.M. and HAZEL, L.N. 1947. Population genetics of a poultry flock under artificial selection. Genetics, 32: 325-339.

LUSH, J.L. 1951. Genetics and animal breeding. Genetics in the 20th Century. New York, Macmillan, 493-525.

MacARTHUR, J.W. 1949. Selection for small and large body size in the house mouse. Genetics, 34: 194-209.

MARTIN, J F.G. and COCKERHAM, C.C. 1960. High speed selection studies. Biometrical Genetics. Pergamon Press. 35-45.

McBRIDE, G. 1959. Assortative mating and selection. Ph.D. Thesis, University of Edinburgh.

MATHER, K. 1941. Variation and selection and polygenic characters. J. of Genetics. 41: 159-193.

MATHER, K. 1942. The balance of polygenic combinations. J. of Genetics, 43: 309-336.

MATHER, K. 1949. Biometrical Genetics. London, Methuen and Co. Ltd. ix + 152 pp.

MATHER, K. 1953. Genetic control of stability in development. Heredity, 7: 297 - 336.

MATHER, K. and HARRISON, B.J. 1949. The manifold effect of selection. Heredity, 3: Part 1. 1-52, 131-162.

OWEN, A.R.G. 1949. The theory of genetical recombination. I. Long-chromosome arms. Proc. Royal Society, B. 136: 67-94.

RASMUSSON, M. 1952. Variation in bristle number of Drosophila melanogaster. Acta Zoologica, Vol. 33-34: 277-307.

REEVE, E.C.R. 1960. Some genetic tests on asymmetry of sterno-pleural chaeta number in Drosophila. Genet. Res. 1: 151-172.

REEVE, E.C.R. and ROBERTSON, F.W. 1953. Studies in quantitative inheritance. II. Analysis of a strain of Drosophila melanogaster selected for long wings. J. Genetics. 51: 276-316.

REEVE, E.C.R. and ROBERTSON, F.W. 1954. Studies in quantitative inheritance. VI. Sternite chaeta number in Drosophila: a metameric quantitative character. Z. Vererbungslehre, 86: 269-288.

ROBERTSON, A. 1950. A preliminary report on the herd of Fulani cattle at Shika, Nigeria. Conference on the improvement of live-stock under Tropical conditions, Dec. 1950, Edinburgh, Scotland. 5 pp. (Mimeograph).

_____ 1952. The effects of inbreeding on the variation due to recessive genes. Genetics. 37: 189-207.

_____ 1955. Selection in animals: synthesis. Cold Spr. Harb. Symp. Quant. Biol. 20: 225-229.

_____ 1960. A theory of limits in artificial selection. Proc. Royal Society, 153, Vol. B: 234-249.

_____ 1961. Inbreeding in artificial selection programmes. Genet. Res. 2, 189-194.

ROBERTSON, F.W. 1955. Selection response and the properties of genetic variation. Cold. Spr. Harb. Symp. Quant. Biol. 20: 166-177.

ROBERTSON, F.W. and REEVE, E.C.R. 1952. Studies in quantitative inheritance. I. The effects of selection of wing and thorax length in Drosophila melanogaster. J. Genetics, 50: 414-448.

SAYER, W. 1937. Feeding and handling experiments on the fusa pedigree sahiwal herd (Third report, 1934-1935). Agric. Live-stock. India. 7: 145-161.

SIERK, C.F. and WINTERS, L.M. 1951. Effectiveness of selection for economically important characters in swine. J. Animal Science. Vol. 10. No.1. 8-12.

STERN, C. 1938. The innervation of setae in Drosophila. Genetics. 23: 172.

STORMENT, C. 1959. On the application of blood group in animal breeding. Proc Xth Int. Cong. Genetics. 1: 206-224.

TANTAWAY, A.O. 1959. Selection limits with sib-matings in Drosophila melanogaster. Genetics : 287-295.

TERRIL, C.E. 1951. Effectiveness of selection for economically important traits of sheep. J. Animal Science, Vol. 10. No. 1: 17-18.

WADDINGTON, C.H. 1952. Canalisation of the development of quantitative characters. Quantitative Inheritance. London. H.M.S.O.

WADDINGTON, C.H. 1957. The Strategy of the Genes. London. Allen and Unwin, Ltd. ix + 262.

WADDINGTON, C.H. GRABER, H. and WOOLF, B. Iso-alleles and response to selection. J. Genetics, 55: 246-250.

WRIGHT, S. 1931.

WRIGHT, S. 1951.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge my indebtedness to:-

The Scientific Research Institute of Mozambique for study leave to carry out this work.

Professor C.H. Waddington, F.R.S. for the provision of facilities in the Institute of Animal Genetics.

Dr. Alan Robertson for encouragement and guidance throughout every stage of this investigation.

Miss J.L. Bloom and Mr. J. Allan for the suggestions, stimulating company, and correction of the manuscript.

All those of this Institute who have contributed much in the way of discussion.